ECOLOGY AND CONSERVATION OF HIGH-ELEVATION AMPHIBIAN POPULATIONS IN HISTORICALLY FISHLESS WATERSHEDS WITH INTRODUCED TROUT

by

David S. Pilliod

A dissertation
submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in the Department of Biological Sciences
Idaho State University

May 2001

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Committee Approval

To the Graduate Faculty:

The members of the committee appointed to examine the dissertation of David S. Pilliod find it satisfactory and recommend that it be accepted.

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ABSTRACT

ECOLOGY AND CONSERVATION OF HIGH-ELEVATION AMPHIBIAN POPULATIONS IN HISTORICALLY FISHLESS WATERSHEDS WITH INTRODUCED TROUT

Dissertation Abstract--Idaho State University (2001)

Introduced trout have often been implicated in the decline of high mountain amphibian populations, but few studies have attempted to understand whether fish stocking also influences the distribution and abundance of amphibians throughout entire mountain basins, including in the remaining fishless lakes. I examined this relationship using the relative abundance of long-toed salamanders (*Ambystoma macrodactylum*) and Columbia spotted frogs (*Rana luteiventris*) in fish-containing and fishless lentic sites in basins with varying levels of historic fish stocking. All lentic waters were surveyed for fish and amphibians in 11 high-elevation basins in the Frank Church - River of No Return Wilderness, Idaho, between 1995 and 1998. I found introduced trout (*Oncorhynchus clarki, O. mykiss, O. m. aguabonita*) in 43 of the 101 sites, representing 90% of the total surface area of lentic water bodies. At the scale of individual water bodies, after accounting for differences in habitat characteristics between fish-containing and fishless sites, the abundance of amphibians at all life stages was significantly lower in lakes with fish. Trout predation is likely responsible for this pattern. At the basin scale, densities of overwintering life stages of amphibians were lower in the fishless sites of basins where more habitat was occupied by trout. Using mark-recapture and radiotelemetry on *R. luteiventris*, I found that many frogs traveled from breeding sites to summer habitats and then to overwintering sites each year. Male frogs usually moved within

100 m of breeding sites, whereas females made annual migrations of more than 2 km (roundtrip) between breeding sites and summer habitats, traveling up to 500 m across dry, uplands. *R. luteiventris* that bred in shallow, fishless wetlands often migrated to deep, fish-containing lakes to overwinter. Trout predation on overwintering *R. luteiventris* may explain why basin fish stocking appeared to negatively affect frog populations in fishless water bodies. These results suggest that many of the remaining fishless habitats are too shallow to provide suitable breeding or overwintering sites for these amphibians and that current trout distributions may eventually result in the extirpation of amphibian populations from entire basins, including water bodies that remain in a fishless condition.

I dedicate this dissertation to

Elena Velasquez, Tobias, and Kova

for their patience, company, and support

PREFACE

Since the 1960s, amphibian populations have been declining in Australia, western Europe, and South, Central, and North America (Houlahan et al. 2000). Concern about amphibian population declines did not culminate until the early 1990s (Blaustein and Wake 1990, Wake 1991), at which point the herpetological community began organizing research to address possible causes of reported declines (Wake and Morowitz 1990). In the last 10 years, research has focused on broad-scale environmental changes, including increased acid precipitation from air pollution (Beebee et al. 1990, Corn and Vertucci 1992), increased ultraviolet B radiation from reduced atmospheric ozone (Blaustein et al. 1994), and climatic changes from global warming (Pounds et al. 1999). Local factors, such as urban development (Delis et al. 1996), wetland destruction (Johnson 1992, Hecnar and M'Closkey 1996), agricultural-chemical runoff (Bishop 1992), and non-native species introductions (Fisher and Shaffer 1996, Knapp and Matthews 2000) also have been identified as important. My research focused one of these local factors: introduced fish.

Non-native fish species have been introduced into nearly all fresh-water ecosystems, including high mountain lakes in some of the most remote wilderness areas in the western United States. Although amphibians evolved with fish predators in permanent, low-elevation waters, fish rarely colonized high-elevation lakes (>800 m) and thus most high mountain amphibian populations were naive to fish predators until fish stocking began in the early 1900s (Bahls 1992). Little is known about the initial effects of fish introductions on amphibian populations in historically fishless watersheds, but historical descriptions from the Sierra Nevada suggest that some amphibian species experienced rapid declines in bodies of water where fish were introduced (Knapp 1996).

In the last 15 years, numerous studies have examined amphibian and non-native fish distributions. Results from these correlational studies have been consistent; amphibian populations are small or absent in water bodies with introduced fish (Bradford 1989, Liss and Larson 1991, Brönmark and Edenhamn 1994, Hecnar and M'Closkey 1997, Bradford et al. 1998, Tyler et al. 1998, Funk and Dunlap 1999, Goodsell and Kats 1999, Knapp and Matthews 2000). Predation is generally considered the cause of observed negative relationships between amphibians and introduced fish, and this is supported by incidental field observations (Emery et al. 1972, Heyer et al. 1975, Semlitsch 1988, Luecke 1990, Liss et al. 1995, Simons 1998). Amphibians are also sensitive to predators in amphibian breeding locations and several studies have shown that some amphibians will avoid ovipositing in water bodies with predators (Resetarits and Wilbur 1991, Kats and Sih 1992, Hopey and Petranka 1994).

Several previous studies have suggested that high mountain amphibians may live in metapopulations and that these population dynamics may influence the response of amphibian communities to introduced trout (Bradford et al. 1993, Tyler et al. 1998, Knapp and Matthews 2000). Amphibians have complex life cycles and thus occupy different habitats and have different habitat requirements depending on their life stage (Wilbur 1980). In addition, many species require distinct habitats seasonally, such as breeding sites, overwintering sites, and foraging areas (Sinsch

1990). If each amphibian population was isolated, then the introduction of trout into one lake would not be expected to affect surrounding amphibian populations. However, if amphibians live in metapopulations or require several distinct habitats, then the introduction of trout into one lake could potentially affect surrounding populations. Taking these scenarios into account, understanding the habitat requirements and movement patterns of amphibians is needed to determine how introduced trout influence amphibian populations and their persistence. In addition, understanding how amphibians use different habitats in a landscape is important for developing management guidelines for high mountain lakes.

The shift in ecological focus from local determinants of species occurrence and abundance to broader spatial scales comes from an increasing awareness of the importance of studying ecological phenomena at spatial and temporal scales that are relevant to the organisms (Turner 1989, Wiens 1989). Although landscapes have no particular scale per se (Allen 1998), in this dissertation, I studied landscapes at the scale of headwater-cirque basins, because this provided a fairly consistent, easily delineated geographical area with clear barriers to dispersal (headwall ridges). For simplicity, I defined a local population as all frogs at a particular lentic site (Goodwin and Fahrig 1998). This simplistic approach appeared to be appropriate at the spatial and temporal scale of this study.

Research Focus

My research was motivated by concern that introduced trout may be threatening amphibian populations in high-elevation lakes and ponds. Funding for this project was initially obtained from the Rocky Mountain Research Station (RMRS, Boise, ID in 1994; ALWRI, Missoula, MT in 1995) to investigate the effects of introduced trout on amphibian populations in wilderness lakes. I chose to focus on Columbia spotted frogs (*Rana luteiventris*) and long-toed salamanders (*Ambystoma macrodactylum*) for my research because they both bred in lentic habitats and they were sufficiently abundant in the study area.

My research approach is outlined in Figure 1. As I began to document the distribution patterns of introduced trout, *R. luteiventris*, and *A. macrodactylum*, I found that simply comparing the presence/absence of amphibians in lakes with and without fish did not represent the complexities of amphibian abundance and habitat use patterns. Therefore, I first documented the habitat use and movement patterns of *R. luteiventris* in Chapter I. I chose to focus on *R. luteiventris* because all post-metamorphic life stages were easy to count, capture, and mark, relative to *A. macrodactylum*. Although *R. luteiventris* had been the focus of several earlier studies (Turner 1960, Licht 1971, Hollenbeck 1974), all had focused on only a few breeding sites and in a relatively small area. In addition, while Turner's study area in Wyoming and Hollenbeck's study area in Montana were considered high-elevation (at 2070 m and 2393 m, respectively), neither area was in steep, mountainous terrain characteristic of the northern Rocky Mountains and my study area. In Chapter I, I used mark-recapture and radiotelemetry to describe the seasonal habitat requirements and movement patterns of *R. luteiventris* in a glacial-cirque basin (Skyhigh Basin), and discussed the results in relation to the distribution of introduced trout.

In Chapter II, I investigated the local (individual water body) and basin-level effects of introduced trout on amphibian populations. For this analysis, I started with simple comparisons of amphibian densities in lentic water bodies (sites) with and without fish. These analyses were considered "local" effects because each site was an independent observation. I then broadened the scale of analysis, by comparing the density of amphibians in fishless sites in basins with varying levels of trout occupancy (percent surface area of lentic habitats occupied by fish per basin). I predicted that if introduced trout only affected amphibian populations in sites with fish, then fishless sites would have similar amphibian densities regardless of how many other sites were occupied by trout in a basin. I found that fishless sites had lower densities of amphibians in basins with more habitat occupied by trout, suggesting that trout were somehow negatively affecting amphibian populations in surrounding fishless sites. I called these basin-level effects because they affected amphibian populations in the entire basin.

To further understand the influence of introduced trout on the population dynamics of amphibians in an entire basin, I investigated the effects of landscape structure on spotted frog populations in Chapter III. This chapter focused on *R. luteiventris* because it required extensive information on habitat use and movement patterns of adults and juveniles, information collected for Chapter I. In Chapter III, I investigated four landscape processes (*sensu* Dunning et al. 1992) in relation to the abundance of frog populations: landscape complementation, landscape supplementation, source-sink dynamics, and neighborhood effects.

Dissertation Organization

All three chapters are written as independent manuscripts. Chapter I, "Habitat use and movement patterns of Columbia spotted frogs (*Rana luteiventris*) in a high mountain basin", was written with Charles R. Peterson and Peter I. Ritson and will be submitted to *Canadian Journal of Zoology*. Chapter II, "Local and basin-level effects of introduced trout on amphibian populations in historically fishless watersheds", was written with Charles R. Peterson and was submitted to the journal *Ecosystems*. Chapter III, "The influence of landscape structure on amphibian population dynamics: a test of Dunning's hypotheses", will be submitted to the journal *Oikos*. The final section of the dissertation is a summary of my major research findings and specific recommendations for wilderness lake managers responsible for the Bighorn Crags area.

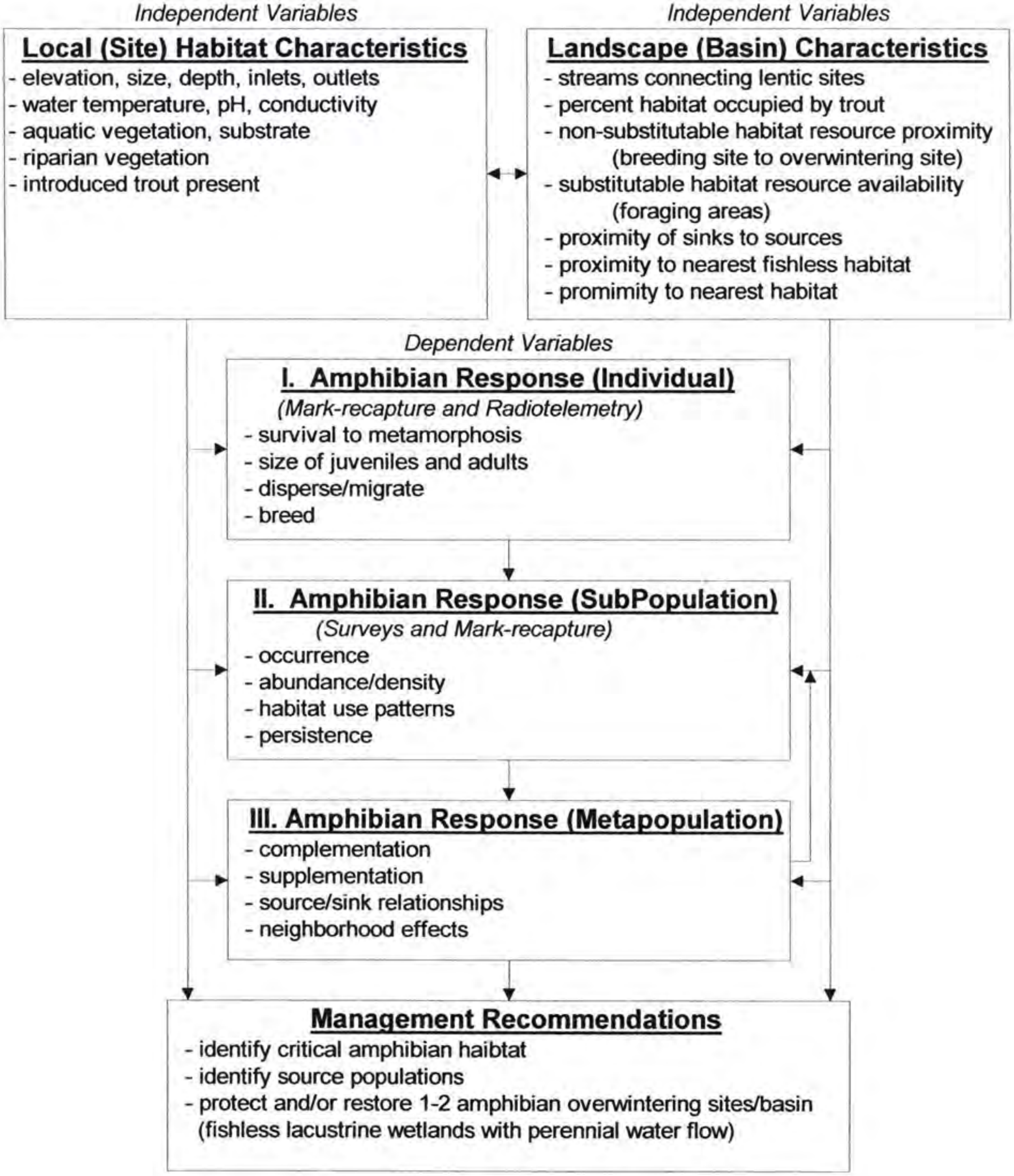


Figure 1. The interaction of factors influencing individuals, sub-populations, and populations (or metapopulations) of amphibians investigated in this study. Roman numerals indicate the three dissertation chapters.

Chapter I. Habitat Use and Movement Patterns of Columbia Spotted Frogs (*Rana luteiventris)* in a High Mountain Basin

ABSTRACT

Existing information on amphibian habitat use and movement patterns is generally inadequate for conservation planning, such as evaluating the connectivity of local populations or identifying potential barriers to dispersal (e.g., introduced predators). This study indicates that *R. luteiventris* living at high altitudes (2323-2634 m) are highly vagile, occupying a variety of habitats at different times of year, including lakes, ponds, flooded meadows, ephemeral pools, and springs in a very short active season (late June-September). Each July, at least 5% of the juvenile frogs, 6% of the male frogs, and 16% of the female frogs that were marked in breeding ponds migrated or dispersed into summer habitats (flooded meadows, springs, lakes). By August, 55% of all female frogs were captured in summer habitats compared to 20% of the male frogs. The few males that dispersed or migrated were captured within 200 m of the breeding sites, while females traveled up to 1100 m from breeding sites to reach summer habitats. In the fall, frogs moved to one of six overwintering sites. Overwintering sites were all deep (>3 m) lakes with perennially flowing outlets and most of which contained introduced trout. To reach overwintering habitats, telemetered frogs followed relatively straight, shortest-travel-distance migration routes, crossing >500 m of dry, upland habitat even when stream corridors were available nearby. This information indicates that introduced trout do not prevent the movement of adult *R. luteiventris* among fishless sites, as has been suggested for other ranid species.

INTRODUCTION

The decline of many amphibian populations over the last several decades is now well documented (Houlahan et al. 2000). As scientists search for global factors to explain regional declines (e.g., climate change, increased UV-B, fungal infections), local habitat destruction, modification, and isolation continue to insidiously reduce many amphibian populations (Alford and Richards 1999, Corn 2000). Despite growing awareness of these local threats to amphibian communities, the development of comprehensive management plans is often hampered by a lack of information on amphibian natural history, especially regarding amphibian habitat requirements and the relevant spatial scales. Managers and policy makers need better information on (1) the seasonal use and movement patterns of animals among different habitats, (2) the spatial distribution of those habitats that are critical for the survival of the animals, and (3) the factors that contribute to habitat loss and fragmentation.

Current understanding of the seasonal movement patterns of anurans is mostly based on drift fence studies (Oldham 1966, Gittins 1983, Pechmann and Semlitsch 1986) and mark-recapture investigations of one or two breeding sites (Blair 1953, Turner 1960, Breckenridge and Tester 1961, Dole 1967, 1971, Breden 1987, Kusano et al. 1995, Patla 1997, Sinsch 1997, Spieler and Linsenmair 1998). Consequently, understanding of the annual habitat use and movement patterns of anurans in a mosaic of lentic habitat patches is poor.

To fully understand anuran habitat use and movements, studies need to include all potential habitats within the dispersal limits of the species. Surveys at the scale of watersheds are important for identifying key breeding, summer, and winter habitat for populations. This information can then be used to protect and manage appropriate and sufficient habitat for population persistence (Pilliod and Peterson 2000).

Although not completely understood, the decline of high-elevation (>800 m) amphibian populations may be associated with habitat loss and fragmentation, despite their "pristine" wilderness setting. Several studies suggest that some high-elevation anuran populations have declined as a result of the loss of suitable breeding and overwintering habitat to introduced trout (Bradford 1989, Knapp and Matthews 2000, Chapter II) and the subsequent increased isolation of remaining frog populations (Bradford et al. 1993). Habitat loss and fragmentation are mostly untested as the proposed mechanisms of decline, reflecting limited but growing knowledge about the habitat use and movement patterns of anurans in high-elevation basins (e.g., Matthews and Pope 1999).

The Columbia spotted frog (*Rana luteiventris*) is one of the most common, lentic-breeding amphibians that is found at high-elevations throughout the northwestern United States and thus was a particularly appropriate species for this study. Among ranids, *R. luteiventris* is fairly well studied, but surprisingly little is known about their habitat requirements at higher elevations, except for a small area in Yellowstone National Park, Wyoming (Turner 1960, Patla 1997). This species is locally threatened in various parts of its range due to the widespread introduction of non-native trout, cattle grazing, water diversions, and habitat fragmentation (Patla 1997, Reaser 2000, Reaser and Pilliod 2002, Chapter II).

The goals of this study were to (1) describe the habitat use and movement patterns of *R. luteiventris*, (2) identify and characterize *R. luteiventris* summer habitats and overwintering sites, (3) determine the migration routes used by *R. luteiventris,* and (4) use this information to evaluate whether introduced trout occupy habitats that are critical for the survival of *R. luteiventris* (hereafter "critical habitats") and/or disrupt the movement patterns of frogs in a high-elevation (2323-2634 m) cirque basin.

METHODS

Study Area

This project was conducted in Skyhigh Basin, a relatively large (1128 ha), glacially formed cirque in a region of the Salmon River Mountains known as the Bighorn Crags. The steep, granitic peaks of the Bighorn Crags rise to 3073 m, forming a crest between the Middle Fork and Main Salmon River drainages in the Frank Church - River of No Return Wilderness (FC-RNRW), Idaho (Figure 1). Skyhigh Basin drains into Wilson Creek, a tributary of the Middle Fork of the Salmon River. The basin contains 16 permanent alpine and subalpine lakes and ponds, 4 flooded meadows, and 5 ephemeral ponds ranging from 2323 to 2634 m in elevation.

The climate in the study area is cool and dry, with 3 to 4 months when surface water is free from ice from mid June to mid October. The region receives approximately 80 cm of precipitation annually, but only about 5 cm falls as rain during the brief summer period (July - August). Most of the surface water comes as a

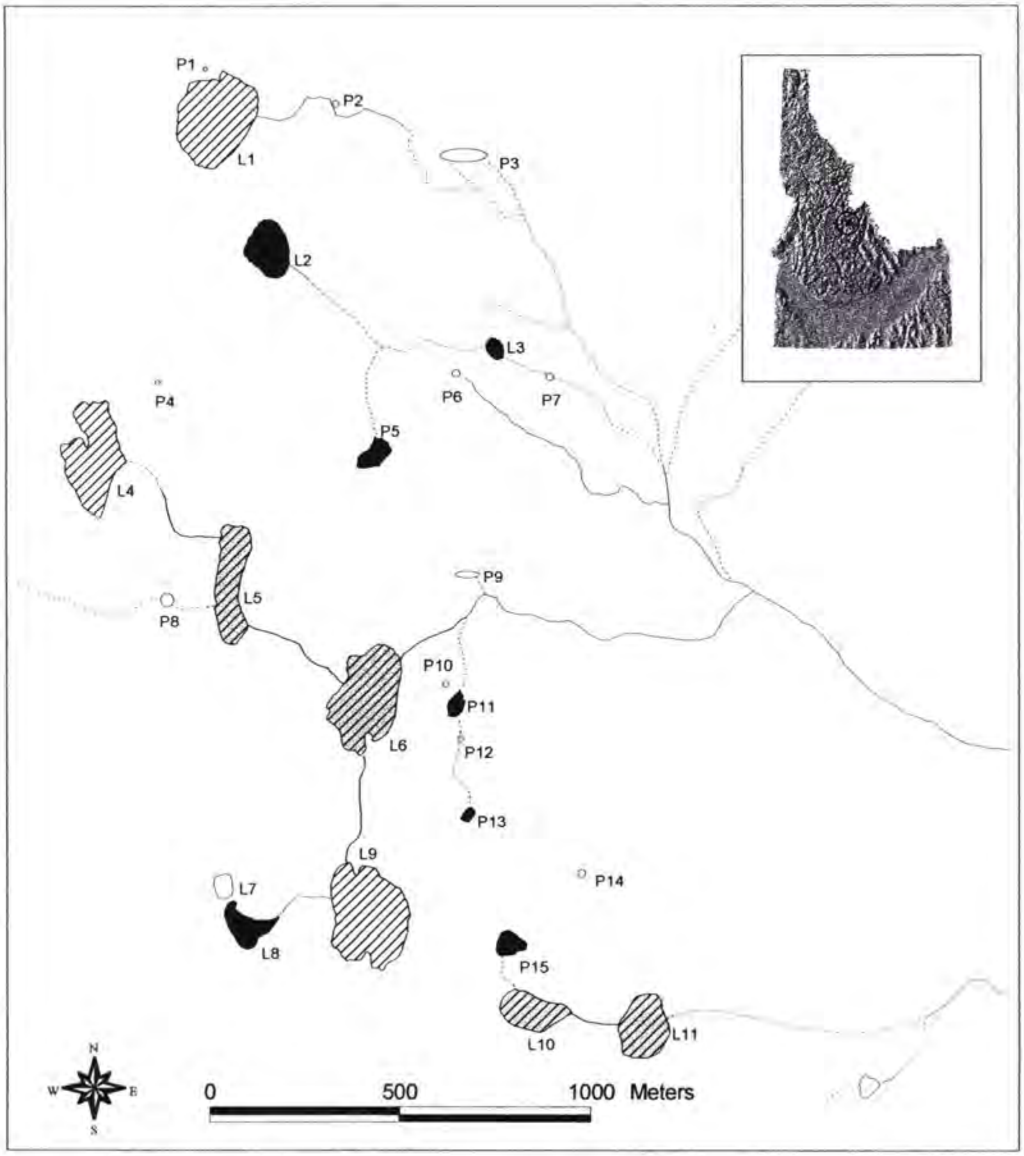


Figure 1. Map of Skyhigh Basin showing the distribution of breeding, summer, and winter habitats with and without introduced trout. Sites are numbered as lacustrine (L1-L11) and palustrine (P1-P15). Breeding (black fill), summer (no fill), and winter (grey fill) *R. luteiventris* habitats are shown. Diagonal lines represent sites with fish. All black filled sites are fishless. Perennial streams are represented by solid lines and intermittent streams (June and July only) by dashed lines. Lake names (from 7.5 minute USGS topographic map) are: Skyhigh (L1), Turquoise (L4), Echo (L5), Reflection (L6), Twin Cove (L9), Doe (L10), Buck (L11), and Fawn (P15).

pulse in the spring when the snowpack, which can reach up to 250 cm deep, begins to melt in late May and June (Finklin 1988). Average daily air temperatures ranged from 10.7-13.0°C in July and August from 1995-98. The basin contained 2 permanent and 6 intermittent first and second-order streams that fed and connected many of the wetlands. These streams reached peak flows during snowmelt in late June, but were mostly dry by the middle of August. Correspondingly, water levels in many lakes dropped as much as 2 m by August and pools in flooded meadows often dried up by mid August.

This cool, dry, subalpine climate results in fairly open forests of subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) with sparse understory vegetation composed mostly of grouse whortleberry (*Vaccinium scoparium*) in the dry uplands and beargrass (*Xerophyllum tenax*) in areas inundated by spring runoff. Engelmann spruce (*Picea engelmanni*), alpine rhododendron (*Rododendrous altiflorum*), and sedges (*Carex*) are found along the margins of lakes and ponds and within flooded meadows and marshy wetlands.

Westslope cutthroat trout (*Oncorhynchus clarki*), rainbow trout (*O. mykiss*), California golden trout (*O. m. aguabonita*), and arctic grayling (*Thymallus arcticus*) were introduced into at least 11 lakes in Skyhigh Basin beginning in 1938. During this study, nine lakes contained trout (*O. clarki, O. mykiss*, and their hybrids). Trout were found in all stream segments to a distance of 500 m downstream from stocked lakes. Prior to the initiation of stocking programs, I believe all lakes and creeks in the basin were most likely fishless due to the steep topography and natural fish barriers (falls) in the tributaries leading into Wilson Creek.

I chose Skyhigh Basin as the study area for this project because it contained several breeding populations of *R. luteiventris* and was relatively undisturbed by human recreation. From 1995-98, *R. luteiventris* bred in the same 7 water bodies in Skyhigh Basin, allowing me to identify breeding sites for the entire study period. The area is protected by wilderness regulations and thus is free from livestock grazing, mechanized recreation (e.g., ATVs), and roads (~12 miles from the nearest trailhead).

Surveys and Marking

All lentic and lotic water bodies in Skyhigh Basin were located and mapped, and lentic habitats were classified as lacustrine or palustrine (Cowardin 1979). All water bodies and streams were surveyed for amphibians and salmonids each July from 1995-98 and in August 1995. Most lentic water bodies were surveyed again in late August and early September 1995-97. All lentic sites were surveyed about twice per year (average, range of 1-9 visits/yr). At each lake and pond, two trained observers conducted visual searches of the entire shoreline. Surveyors walked approximately 2 m apart, with one person in the water and a second person on the shore. Observers searched streams by walking their entire length, one observer along each bank (usually within 2 m of each other). The entire area of meadows was searched in a zigzag pattern (Thoms et al. 1997). Where aquatic or terrestrial grasses and sedges were present, dip nets were used to sweep the vegetation for frogs.

At each site, I attempted to capture all of the frogs observed. Frogs were captured by hand or net, held in nets or nylon bags for 2-15 minutes while handling, and released at the capture location. For each frog captured, snout-vent length was measured with calipers (SVL, ±2 mm), weight was measured with a Pesola spring scale (±0.5 g), and sex of frogs >46 mm was determined by the presence of nuptial pads on males. Based on size, weight, and sexual maturity, I grouped individuals into three size classes (metamorph, <20 mm; juvenile, 20-46 mm; adult, >46 mm).

To document gross movement of frogs among habitats, I marked as many juvenile and adult frogs as possible at each lotic and lentic water body from 1995 to 1997. I did not mark young-of-the-year metamorphosing frogs as they emerged from the breeding ponds, because I did not want to increase mortality during this stressful time in their life history. Frogs captured at breeding sites (excluding metamorphs) were marked with a site-specific toe-clip pattern to identify the location at first capture. To differentiate between frog dispersal and seasonal migrations, I marked frogs in summer habitats with individual codes and recorded recapture locations. In addition, all frogs that were originally marked at breeding sites and were then recaptured at a new site, were given an additional toe-clip to differentiate them from other frogs in the event they returned to the site where they were originally marked. Recaptured frogs were handled as above and toe codes were recorded. To compare the distance traveled by dispersing male and female frogs, I reported the percent of males or females captured at 200 m intervals from the breeding sites approximately four weeks after initial marking in 1995.

Toe-clip patterns were modified from Donnelly (1989). I clipped two toes per frog captured at breeding sites and always on different limbs. Frogs captured in summer habitats had three toes clipped, but no more than two toes on any one limb. Thumbs were not clipped. I clipped toes at the second tarsal or carpal joint with finepoint, electrical wire clippers or stainless steel cuticle clippers disinfected with a 70% isopropyl alcohol swab. Because the greatest potential for marking errors was right-left confusions, I only included frog movements between sites that could not have been a right-left marking error. This was a conservative approach to reduce error rates. Thus, the movement results presented are minimum estimates of actual movement rates.

To determine the seasonal habitat use patterns of frogs, I compared observation rates and capture records of marked *R. luteiventris* in lentic and lotic habitats in Skyhigh Basin. Breeding habitats were identified by the presence of egg masses and tadpoles. Based on seasonal occupation, lentic sites were further identified as summer or fall/winter habitats. To summarize habitat use data, I first summed the maximum number of juvenile, male, and female frogs captured in lacustrine (deep lakes without fish, deep lakes with fish), palustrine (shallow ponds, ephemeral ponds, flooded meadows), and riverine (creeks without fish, creeks with fish) habitats in each year from 1995 to 1998. To calculate percent captured by age (juvenile or adult) in each of these habitats, I divided the number captured in each habitat by the total number captured each year. To calculate the percent of individuals dispersing from breeding and summer habitats, I first calculated the cumulative number of juvenile, male, or female *R. luteiventris* captured and marked in breeding and summer habitats. Then, I divided the number of individuals that dispersed >100 m from each of the breeding and summer habitats by the cumulative number frogs marked at the breeding and summer habitats up to that point in time; juveniles, males, and females were treated separately. To calculate the percent of individuals recaptured at breeding and summer habitats where first marked (did not disperse), I divided the number of *R. luteiventris* recaptured at each habitat type by the cumulative number of frogs marked at the breeding or summer habitats up to that point in time. To show differences between male and female frogs in their seasonal use of habitats, I divided the number of male or female frogs captured in either breeding or summer habitats in July surveys each year by the total number of frogs captured in July surveys each year. I plotted this against the percent of male or female frogs captured in breeding versus summer habitats in August 1995.

Radiotelemetry

Radiotelemetry was used to study the movement patterns and activity areas of *R. luteiventris* between the months of July and September from 1995 to 1997. The selection of frogs to be telemetered was not random, and my site selection and frog weight limitation criteria resulted in biasing my telemetry study toward female frogs. I intentionally placed more transmitters on frogs in summer habitats, such as flooded meadows, to increase my chance of observing movement. This selection likely underestimated the total distance traveled per season. To reduce the effect of the transmitter on frog mobility and behavior, I did not place transmitters on any frogs less than 26 g. This weight cut-off was an attempt to limit the combined weight of the transmitter and harness (approximately 1.6 g) to less than 5% of the frog's body weight.

I attached radio transmitters (BD-2T transmitters, Holohil Systems Ltd., Ontario, Canada) to 87 adult *R. luteiventris*, including 81 females (65-85 mm SVL, 26-65 g) and six males (51-73 mm SVL, 26-34 g) between July and September 1995 to 1997. Frogs carried transmitters for an average of 24 days (range of 2-57). An additional 29 frogs (3 in 1995, 4 in 1996, and 22 in 1997) were excluded from the analyses because they dropped their transmitter and harness before being relocated. The transmitters were attached to the frogs using a lightweight belt-type harness made from a variety of materials including surgical polyethylene tubing (Bartelt and Peterson 2001), nylon ribbon, rayon cord, or polyester ribbon. The belt fit around the waist of the frog in the skin fold created by the femoral-coxa articulation.

I located telemetered frogs every 1-3 days with a Telonics TR4 or TR2 receiver (Telonics, Inc., Mesa, AZ) and an "H" directional antenna. Initial frog locations, final locations, and all movements greater than 100 m were determined using a differentially correctable global positioning system (GPS, GeoExplorer II, Trimble Electronics, Sunnyvale, CA). I mapped shorter movements using a compass and 30 m tape. To avoid excessive injury to the frogs, I captured telemetered frogs weekly to check for abrasions or lacerations caused by the transmitter harness. Abrasions were treated with Neosporin ointment and often healed without further complications. If lacerations penetrated the skin, the harness and transmitter were removed.

Habitat Data Collection

To characterize breeding, summer, and winter habitats, I collected and summarized data on habitat variables that I considered important to amphibians. I recorded elevation from 1:24,000 USGS topographic maps and surface area from aerial photographs in a geographic information system (ArcView 3.1, ESRI). Maximum water depth was based on bathymetric transects of each lentic site using a hand-held sonar or tape measure for very shallow sites. At each visit to a water body, I recorded shoreline water temperature at 1 m from shore and 5 cm from the surface using a mercury thermometer. For analysis, I used average water temperature per site across all visits. I collected pH and conductivity data, but these measurements did not vary much among sites. I estimated the percent shoreline cover by mapping the vegetation along the shoreline and then dividing the total amount (meters of shoreline) of each vegetation type by the total perimeter of the site. A similar approach was used for aquatic substrate. For flooded meadows, I visually estimated the percent cover of the area. Finally, I recorded the presence of perennially flowing springs, inlets, and outlets.

Statistical Analysis

For statistical analyses, decisions to use non-parametric alternatives to parametric tests were based on violations of homogeneity and normality of error variances. To compare measured habitat variables among breeding sites, summer habitats, and overwintering sites, I used a Kruskal-Wallis test (non-parametric). To reduce the number of habitat variables compared, I created two composite factors of the habitat variables using a Principal Components Analysis (PCA) with Varimax rotation. To avoid redundancy between variables, elevation (correlated with water temperature) and surface area (correlated with depth) were not included in the PCA.

To test for habitat differences among breeding sites, summer range, and winter range, I used Analysis of Variance (ANOVA) with factor scores as my independent variable.

To compare the distance traveled by recaptured male and female frogs in 1995, I used a Mann-Whitney U Test (non-parametric). However, because animal size can influence mobility, the distance traveled was regressed on the SVL of each frog that dispersed in 1995. To control for the influence of size differences between male and female frogs, I compared differences in the distance traveled by each sex using only male and female frogs of similar size (58-70 mm SVL) in an ANOVA. I did not use circular statistics in my analyses of frog dispersal direction because of inadequate numbers of capture locations. All statistical tests were performed on SPSS v.10.0 (SPSS Inc, Chicago, IL). I determined statistical significance based on a <0.05 probability criterion.

RESULTS

Habitat Use

From 1995 to 1998, a total of 736 post-metamorphic *R. luteiventris* were captured and marked in 24 of 27 lentic sites and 7 of 8 streams in Skyhigh Basin. *R. luteiventris* occupied lakes, ponds, flooded meadows, ephemeral pools, springs, and streams, including waters containing introduced trout (Figure 2). One site (L3, a deep, fishless lake) contained the majority of frogs in Skyhigh Basin, representing from 11-64% of the juvenile frogs and from 48-69% of the adult frogs captured in any year (Figure 2). Through repeated, comprehensive surveying of Skyhigh Basin, mark-recapture, and radiotelemetry, I identified 7 breeding sites, 13 summer habitats,

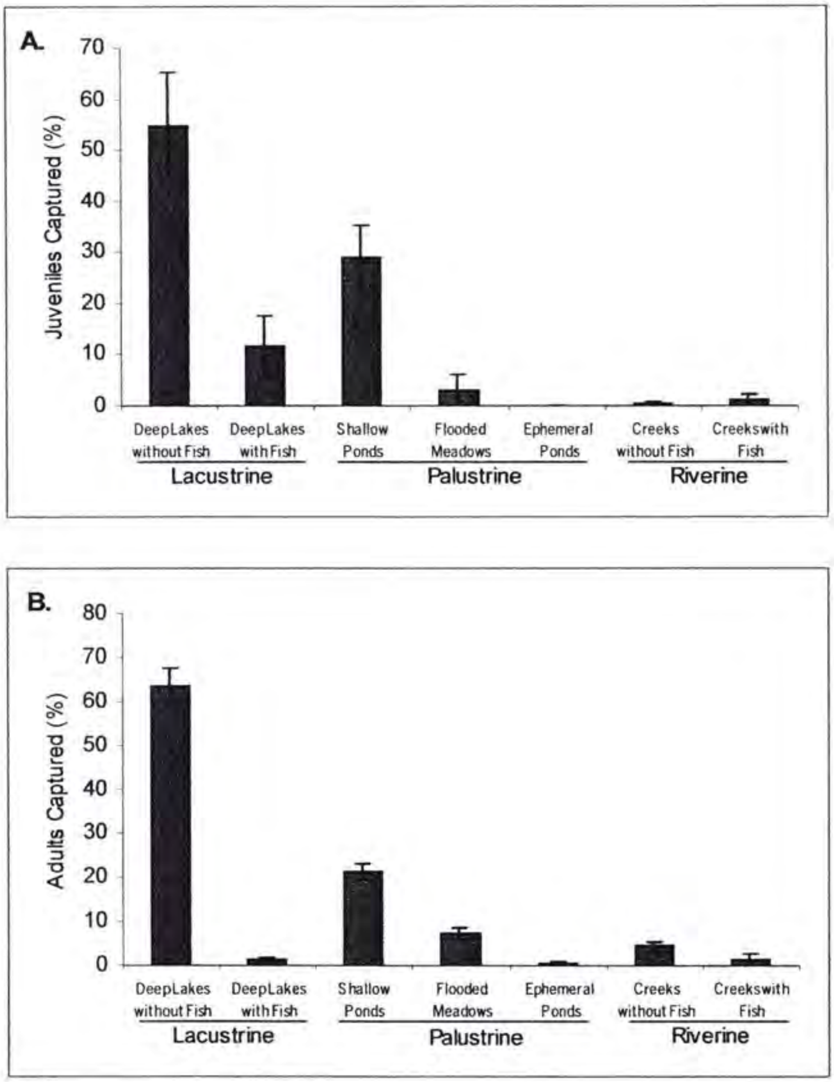


Figure 2. The average percent of juvenile (A) and adult (B) *Rana luteiventris* captured each year in different habitat types in Skyhigh Basin between 1 July and 15 August 1995-98. Yearly variation is shown as standard error bars (±1 SE). The bar representing deep lakes without fish is mostly composed of frogs from site L3. On average, site L3 contained 33% of the juvenile and 61% of the adult frogs in Skyhigh Basin.

and 6 overwintering sites (see Figure 1). Table 1 summarizes the characteristics of these breeding, summer, and winter habitats. The Kruskal-Wallis probability values indicate that summer habitats were the smallest, most shallow sites, while breeding and overwintering habitats were progressively larger and deeper (all >3m). In addition, all breeding sites were fishless, while 4 out of 6 overwintering sites contained introduced trout. All overwintering sites also had perennially flowing outlets.

To further characterize the seasonal habitat associations of *R. luteiventris*, I created composite factors of the measured habitat variables. Two composite factors explained 60% of the variability in the measured habitat variables. Factor 1 explained 31% of the variability in habitat and characterized deep, rocky lakes with fish, shrub-covered shorelines, and perennially flowing outlet streams. This factor was associated with overwintering sites (Figure 3). Factor 2 explained an additional 29% of the variance in habitat and characterized warm ponds with grass or sedge-covered shorelines, emergent sedges, silt substrate, and perennially flowing inlets or springs. This factor was associated with L3, the largest frog population in the basin and one of two sites that was both a breeding site and overwintering site (Figure 3). The other breeding/winter site (L8) more closely resembled the other breeding sites and did not support many frogs at any time of year. Winter habitats were significantly different from breeding habitats across Factor 1 ($F_{1,2}$=5.495, P=0.013). Aquatic habitats used exclusively during the summer were highly variable across factor 2 (not shown), but tended to be smaller, shallower sites compared with winter habitats (Table 1).

Table 1. Median and range (in parentheses) of breeding, summer, and winter habitat variables for *Rana luteiventris* in Skyhigh Basin, Frank Church - River of No Return Wilderness, Idaho. Kruskal-Wallis probability values indicate significant differences among breeding, summer, and winter habitat for each habitat variable.

Habitat Variable	Breeding Habitat (N=7)		Summer Habitat (N=13)		Winter Habitat (N=6)		K-W *P*
Elevation (m)	2505	(2463-2606)	2549	(2463-2634)	2478	(2463-2585)	0.408
Surface Area (ha)	0.39	(0.10-1.30)	0.02	(0.003-4.29)	1.51	(0.02-3.68)	0.024
Maximum Depth (m)	3.1	(1.6-12.4)	0.4	(0.2-24.3)	8.4	(3.1-12.4)	0.013
Water Temperature (^{o}C)	16.3	(13.8-20.7)	14.8	(9.7-24.0)	16.3	(13.5-20.7)	0.863
Forested Shoreline (%)	38	(0-86)	30	(0-93)	27	(0-68)	0.999
Shrub Shoreline (%)	15	(0-59)	0	(0-70)	40	(0-61)	0.150
Grass/Sedge Shoreline (%)	5	(0-100)	10	(0-100)	8	(0-100)	0.692
Rock Substrate (%)	5	(0-100)	0	(0-100)	50	(0-100)	0.078
Silt Substrate (%)	74	(0-100)	100	(0-100)	46	(0-100)	0.114
Emergent Vegetation (%)	10	(0-50)	20	(0-100)	39	(0-54)	0.483

Most juvenile frogs were captured at breeding sites and a few were captured up to 350 m from breeding sites (Figure 4A). Each year, approximately 5% of the juvenile frogs marked at the breeding sites were recaptured in summer or winter

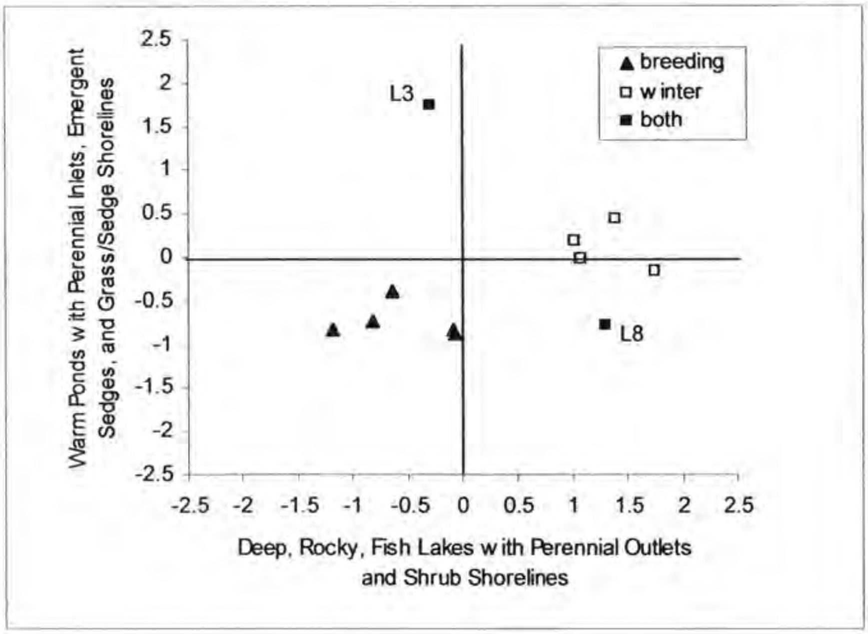


Figure 3. Plot of Factor 1 (deep, rocky, fish lakes with perennially flowing outlets and shrub shorelines) versus Factor 2 (warm ponds with perennially flowing inlets, emergent sedges, and grass/sedge shorelines) from a PCA of measured habitat variables in all sites where frogs were found in Skyhigh Basin. Breeding sites are represented by filled symbols and overwintering sites are represented by squares. Sites L3 and L8 were both breeding and overwintering sites. Summer habitats are not shown.

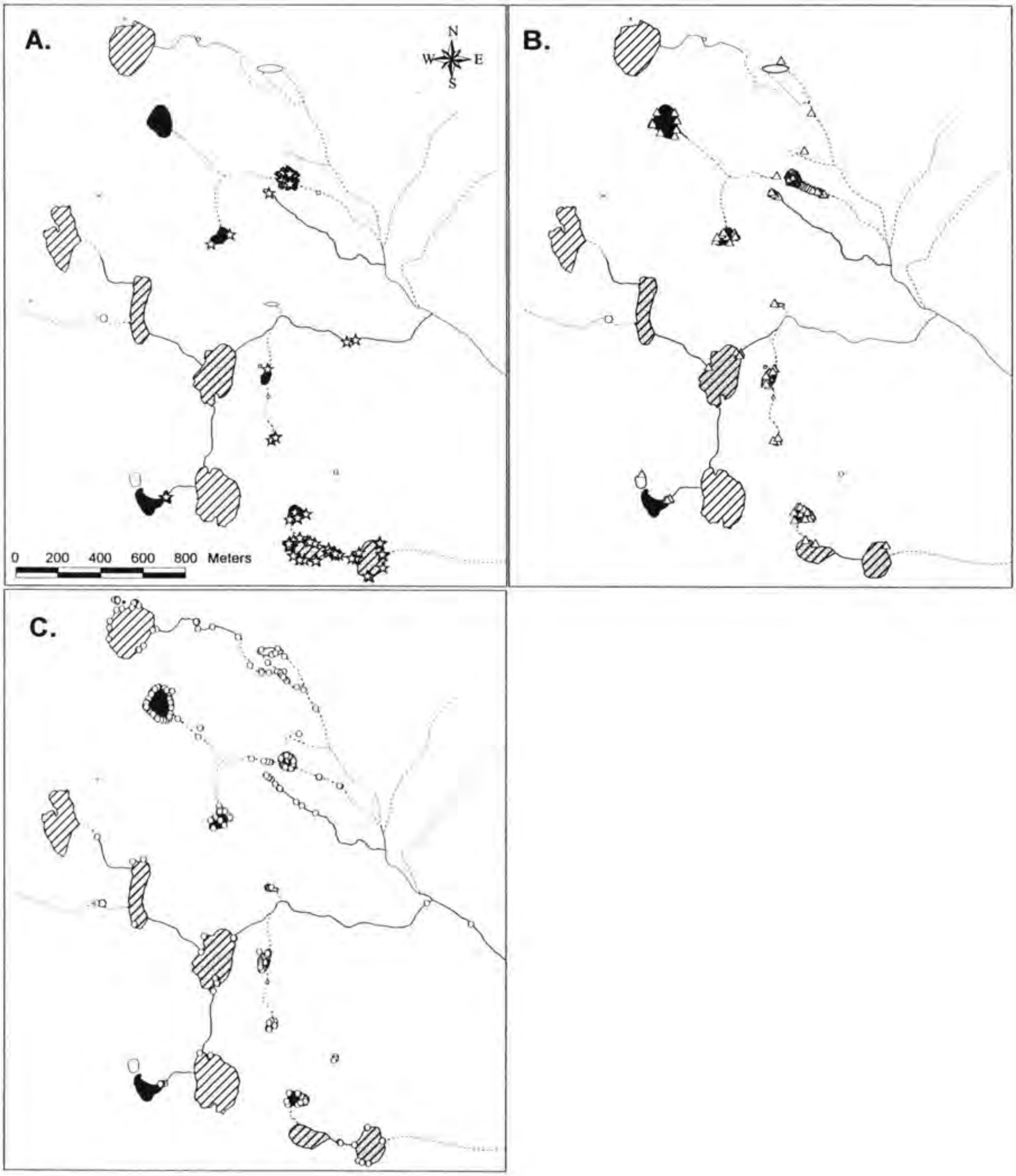


Figure 4. Map of Skyhigh Basin study area showing *Rana luteiventris* capture locations. Panel A shows the distribution of juvenile frogs >1 year old (stars). Panel B shows the distribution of male frogs (triangles). Panel C shows the distribution of female frogs (circles). Note: the open circles in panels A and B are ponds and not male frogs. The lentic habitat fill patterns are consistent in all panels and described in Figure 1.

Table 2. Summary of the total number of juvenile, male, and female *Rana luteiventris* marked and captured in breeding sites and summer habitat in Skyhigh Basin from July 1995 to July 1998. The average annual percentages of frogs recaptured at sites where marked or dispersed >100 m from initial capture locations are shown. Ranges are in parentheses.

Frogs First Captured in:	Breeding Habitat			Summer Habitat		
	Juveniles	Males	Females	Juveniles	Males	Females
Total Marked	124	294	154	54	25	85
Total Captures	177	615	339	69	32	219
Recapture/yr (%)	26	66	56	12	9	43
	(10-42)	(52-74)	(52-61)	(0-20)	(0-20)	(29-51)
Dispersal or Migration/yr (%)	5	6	16	0	18	34
	(0-20)	(3-9)	(9-23)	0	(0-50)	(6-47)

habitats (Table 2). Unlike adults, juvenile frogs remained in some winter habitats even during summer months. In September 1997, I observed a mass migration of 26 recently metamorphosed frogs (~20 mm SVL, ~0.8 g) from a shallow breeding pond (P15) into a nearby lake with introduced trout (L11). To reach the lake, frogs dispersed about 100 m over dry land and 350 m total distance. In 1995, I captured numerous juvenile frogs in L10 and L11. However, none of these frogs had returned to P15 as adults by 1998. Of 54 juvenile frogs marked in L10 and L11, only 11% (6) were recaptured in the same year and only 2% (1) were recaptured in two consecutive years. From 1995 to 1998, I did not observe further movement of juvenile frogs from L10 and L11 or from summer habitats where captured (Table 2).

R. luteiventris habitat utilization and seasonal activity patterns were variable between sexes. Males were mostly captured at or near breeding sites (Figure 4B), while females were more widely distributed (Figure 4C). Each year, about 6% of the male and 16% of the female frogs that were marked at the breeding sites were recaptured in summer habitats (Table 2). Summer habitats were occupied from early

July to late August and included large lakes, small ponds, flooded meadows, ephemeral ponds, springs, and pools along small streams. Greater numbers of females than males occupied these summer habitats (Figure 5) and greater proportions (up to 51%) of females marked in these summer habitats were recaptured (Table 2). This pattern was consistent among years.

Site Fidelity

Both sexes showed strong site fidelity to breeding sites, while only females tended to return to their summer habitats. From 1995-98, about 66% of the males and 56% of the females marked in breeding sites were recaptured in subsequent years, while only 9% of the male and 43% of the female frogs were recaptured in subsequent years in the summer habitats where they were originally marked (Table 2). Of 32 individually marked female frogs in P3 (a site where females congregated in the summer), I found that up to 75% (24) returned each year. Conversely, only 15% (2/15) of individually marked male frogs were recaptured in P6 and P7 in subsequent years (two sites where male frogs congregated in the summer).

Migration to Summer Habitat

Male and female frogs dispersed different distances from breeding ponds and consequently occupied different summer ranges. Figure 6 illustrates the dispersal distances traveled by male and female frogs only 4 weeks after I initially marked frogs in Skyhigh Basin in 1995. Males tended to stay close to breeding sites and thus occupied a narrower range of habitats, predominantly associated with streams flowing

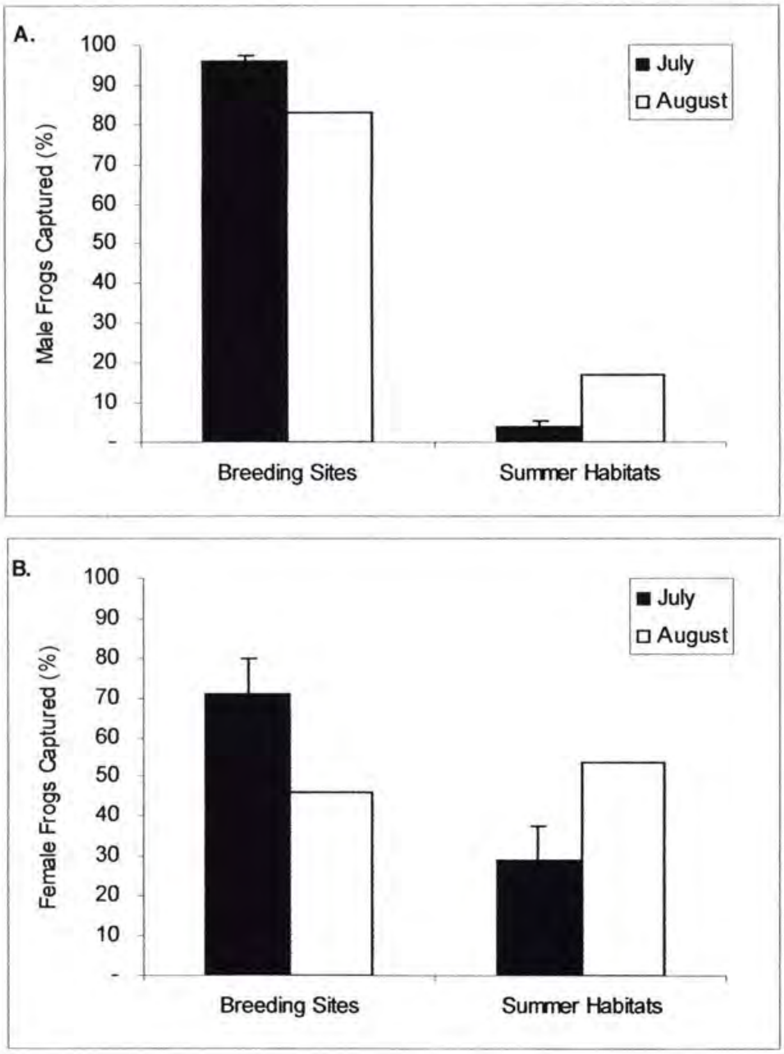


Figure 5. The proportion of all male (A) or female (B) *Rana luteiventris* captures in each survey period that were located in breeding or summer habitats in July 1995-98 (filled bars) and August 1995 (open bars) in Skyhigh Basin, FCRNRW. Among year variation in July captures (1995-98) are displayed as standard error bars.

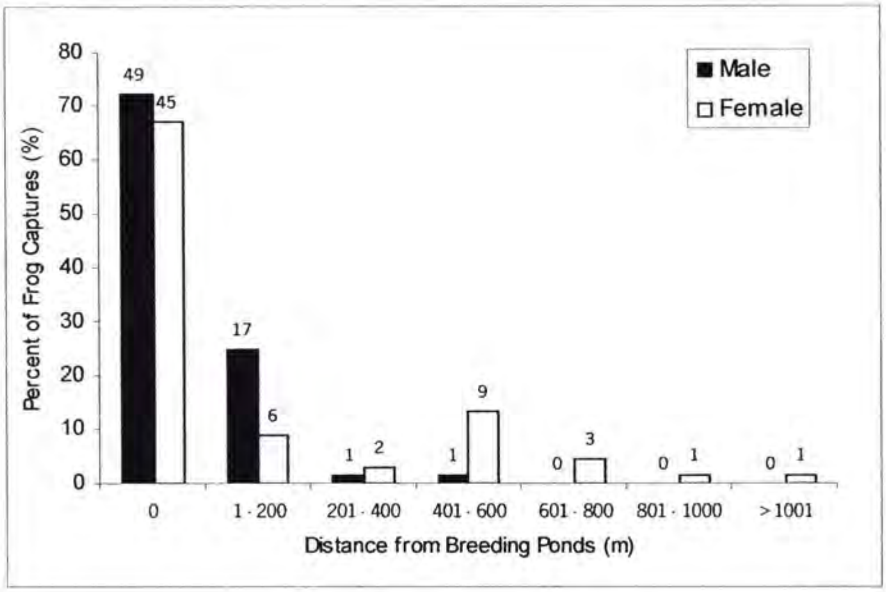
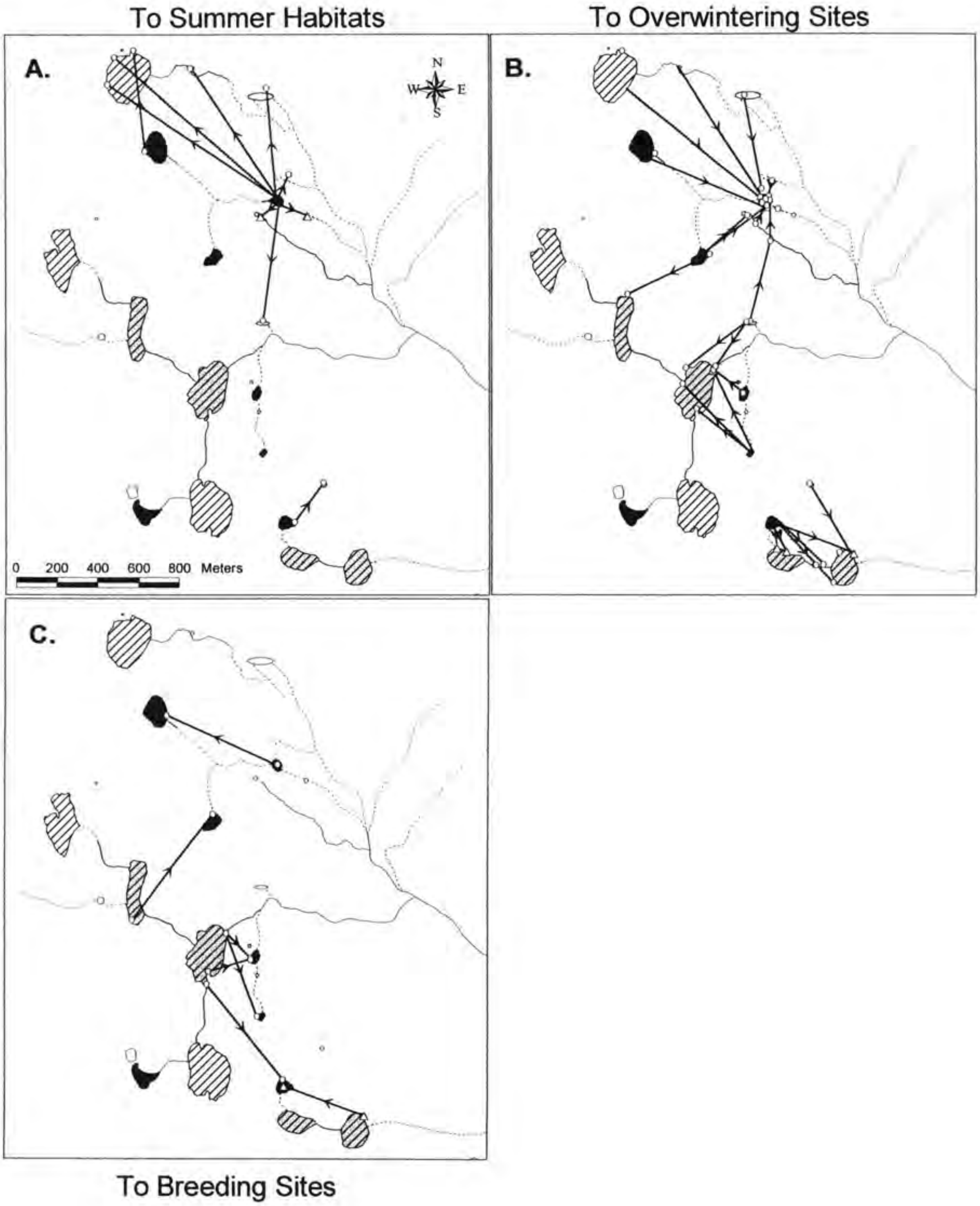


Figure 6. Dispersal of male (filled bars) and female (open bars) *Rana luteiventris* from 7 breeding ponds in Skyhigh Basin between 10 July and 1 September 1995. The numbers above each bar represent the number of frogs in each category.

out of or within 100-200 m of the breeding ponds (Figure 7A). Males are capable of dispersing as far as females, as indicated by one male's dispersal of 900 m from the breeding pond where it was marked (P11) and was captured in two consecutive years at another breeding site (L3), but normal male dispersal was much shorter. In general, females that dispersed from the breeding ponds generally traveled much longer distances than males, from 100-1100 m distance from the breeding ponds (Figure 6). Female summer habitats included large lakes, small ponds, wet meadows, and forested springs (Figure 7A). Frogs marked at the same breeding site did not all move to the same summer range. For example, frogs marked at L3 were recaptured in many different sites (Figure 7A).



To Summer Habitats

To Overwintering Sites

To Breeding Sites

Figure 7. Maps of migration patterns (straight lines between recapture locations) from breeding sites to summer ranges in early July (A), from breeding sites and summer ranges to overwintering sites in late August and September (B), and from overwintering sites to breeding sites in late June and early July (C) in Skyhigh Basin, 1995 and 1998. Frog symbols and site fill patterns are the same as those used in Figs. 1 and 4.

Migration to Fall/Winter Habitat

Beginning in mid August and continuing until late September, adult frogs began migrating from breeding sites and summer habitats to overwintering sites (Figure 7B). During September surveys of overwintering sites, frogs were usually found at the inlets or outlets. In L3, I could not identify one area of the lake where frogs were congregating, but the numerous springs in and around the lake probably provided suitable overwintering locations. In addition, some frogs may have used a spring associated with P6, which was only ~120 m away (Figure 7B).

Although most of the frogs in a particular site migrated to the same overwintering area, some individuals moved to completely different locations to overwinter. For example, one frog at P5 migrated to and overwintered at L5 in 1995 and 1997, while other frogs in P5 moved down to L3 to overwinter (Figure 7B). While most male and some female frogs had to migrate 450 m or less between the breeding and overwintering sites (up to 900 m annually), female frogs that had migrated to distant summer ranges had to make long-distance return migrations to reach overwintering sites in the fall. The longest annual female migration observed was over 2200 m round-trip, between sites L3 and L1.

Telemetered frogs migrated more often at night and during rain events, but also migrated during the day and during dry periods. While crossing about 500 m of dry, forested habitat, one female frog used a rodent burrow near a large boulder to rest during the day before continuing and completing the migration the following night.

Activity Ranges of Migratory Frogs

Based on recapture locations of 28 migratory female frogs that were individually marked or telemetered, and had at least 5 captures over at least 365 days, I calculated median minimum convex polygon "activity" ranges of 2.47 ha (0.14-26.34 ha). I did not have enough migrating male captures to calculate "activity" ranges for male frogs.

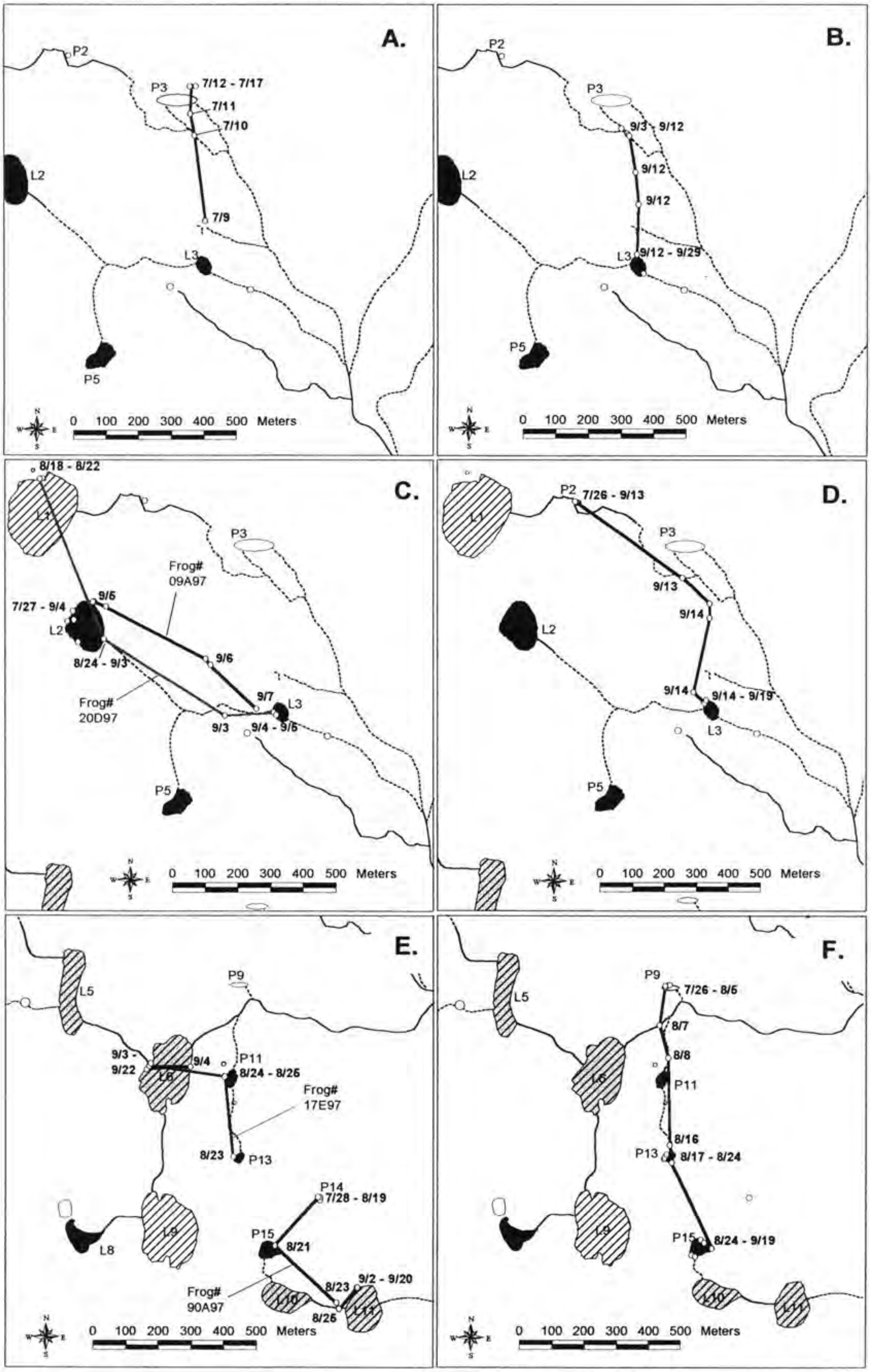
Rates of Travel

Depending on the distances between summer and fall ranges (from 100 to 1100 m), frogs completed their migrations in 1 - 2 days, traveling up to 708 m in a day. Of the frogs with transmitters, 8 of the 10 fastest migration rates (50 - 160 m/hr) were observed between 2000 and 0645 when air temperatures were between 3 and 10°C and rain was either falling or had been falling in the previous 24 hours.

Travel Routes

I observed migration behavior in 37 telemetered *R. luteiventris*, but only 13 were captured during the migration. All others completed migrations too quickly to be captured while migrating between summer and winter habitats (<24 hours). Based on these 13 female frogs, travel routes were fairly direct, closely approximating the shortest linear distances (Figures 8A and B). Frogs that migrated to summer habitats in the spring (N=2 observations; Figure 8A) followed similar routes back to winter habitats in the fall (N=6 observations, Figure 8B). Stream corridors were followed when streams flowed along the migratory route, but for the most part, frogs did not follow streams. For example, female frogs used a combination of streams and terrestrial routes across dry land to move from L1 to L3 (Figure 8C) and from P2 to L3 (Figure 8D), instead of migrating along the entire length of the streams that connected these sites. By using "shortest distance" stream/terrestrial travel routes, instead of only following the streams, these frogs reduced their travel distance by more than 1 km. This migratory behavior resulted in frogs traveling at least 500 m across dry, upland habitat, through sub-alpine fir and lodgepole pine forests with sparse grouse whortleberry and bear grass understory vegetation. When available, frogs used seeps, springs, lakes, and isolated pools of intermittent streams when traveling between distant habitats that lacked direct stream connections (Figures 8E and F).

Figure 8. Examples of *Rana luteiventris* migration routes and timing of migration in Skyhigh Basin based on locations of 8 telemetered female frogs in 1996 and 1997. Frog symbols and site fill patterns are the same as those used in Figs. 1 and 4.


A.
P2
P3
7/12 - 7/17
7/11
7/10
L2
7/9
L3
P5
0 100 200 300 400 500 Meters
B.
P2
P3
9/3 - 9/12
9/12
9/12
L2
L3
9/12 - 9/25
P5
0 100 200 300 400 500 Meters
C.
8/18 - 8/22
L1
P3
Frog#
09A97
9/5
7/27 - 9/4
L2
9/6
8/24 - 9/3
Frog#
20D97
9/7
L3
9/3
9/4 - 9/5
P5
0 100 200 300 400 500 Meters
D.
L1
P2
7/26 - 9/13
P3
9/13
9/14
L2
9/14
9/14 - 9/19
L3
P5
0 100 200 300 400 500 Meters
E.
L5
P9
9/3 -
9/22
9/4
P11
8/24 - 8/26
L6
Frog#
17E97
8/23
P13
P14
7/28 - 8/19
L9
L8
P15
8/21
8/23
9/2 - 9/20
Frog#
90A97
L10
8/26
L11
0 100 200 300 400 500 Meters
F.
P9
7/26 - 8/5
L5
8/7
8/8
L6
P11
8/16
P13
8/17 - 8/24
L9
P15
8/24 - 9/19
L10
L11
0 100 200 300 400 500 Meters

DISCUSSION

The most important result of this study is that *R. luteiventris* move among distant lacustrine and palustrine wetlands at different times of year using a combination of terrestrial upland and riparian travel routes. The observed habitat use and movement patterns have important implications for the conservation of montane *R. luteiventris* populations in relation to their habitat requirements and recolonization abilities.

Habitat Use

Although I suspected *R. luteiventris* was highly vagile based on the variety of habitats occupied in Skyhigh Basin, I were surprised by the amount and rate of frog movements. Considering that the juvenile and adult frogs captured and marked in the 19 summer and winter habitats probably came from one of the seven breeding ponds originally (breeding occurred in the same 7 sites from 1995 to 1998), my calculations of dispersal rates from breeding sites (Table 2) are conservative. If I assume that unmarked individuals captured at summer habitats in July 1995 had already dispersed from one of the breeding sites that year, then my estimates of dispersal from breeding ponds increase to 33% for juvenile frogs, 17% for male frogs, and 47% for female frogs (calculated, by sex or life stage, as the # marked frogs that moved to summer habitats + # unmarked at summer habitats / # marked in breeding sites + # unmarked in summer habitat). In support of this assumption, I rarely found frogs during the earliest surveys of summer habitats in the spring but subsequently encountered steadily increasing numbers of frogs at these sites through the summer. In mid

August, this pattern was reversed, with steadily increasing numbers of frogs at overwintering sites. Furthermore, the arrival of frogs at overwintering sites coincided with the migration of telemetered frogs from breeding and summer habitats to overwintering sites.

Migration to Summer Habitat

The migratory behavior of *R. luteiventris* in Skyhigh Basin suggests that the habitat requirements of this species vary seasonally. The spatial arrangement of breeding, foraging, and overwintering sites in Skyhigh Basin probably resulted in annual migrations of male and female frogs. Only one site appeared to meet all of the seasonal habitat requirements of the species (L3) and this site was noticeably different than the other breeding and overwintering habitats in the basin (Figure 3). Still, frogs migrated annually from this site to reach other summer ranges. The long-distance summer migrations (500-1000 m) completed by female frogs in L3 and other sites may have been associated with efforts to reach high quality foraging habitat or areas with less competition, perhaps especially important due to the short active season in this harsh climate. The difference in distance traveled by males and females supports this hypothesis, because males require less energy annually than reproductive females. A female *R. luteiventris* loses 25-35% of her body mass during egg deposition (J. Engle, personal communication), and must regain this loss before reproducing again. Differences in migratory distance between sexes may also be a function of size, because larger frogs moved longer distances from the breeding ponds ($F_{1,79}$=32.07, $P<0.01$). When males (N=12) and females (N=16) of similar size

(58-70 mm SVL), but likely dissimilar age, were compared, there was no difference in migratory distances between sexes. This implies that long-distance annual migrations may only be possible for larger females (and thus probably older females). However, I suspect that migration distance is more related to behavioral than morphological or physiological differences between the sexes. In an adjacent basin, an adult male (27 g, 60 mm) traveled 1505 m between lakes. His dispersal path involved a 75 m drop in elevation and a 150 m gain in elevation along an almost entirely terrestrial route.

Post-spawning anurans have been found to migrate considerable distances from breeding ponds. Terrestrial species, like the common toad (*Bufo bufo*) and boreal toad (*Bufo boreas*), may travel 2-3 km from breeding ponds into summer ranges (Sinsch 1987, Bartelt 2000). Ranids have generally been considered less mobile than other anurans, especially across upland habitats (Sinsch 1990), but recent information on ranid dispersal indicates capabilities similar to bufonids (see Table 1 in Dodd 1996). In the Midwestern U.S., adult leopard frogs (*Rana pipiens*) were found to travel up to 1.5 km over land (Oldfield and Moriarty 1994). Adult wood frogs (*Rana sylvatica*) disperse up to 1.6 km in Virginia (Berven and Grudzien 1990). In Oregon, marked adult northern red-legged frogs (*Rana aurora*) have been found 2.6 km from their release site (Hayes et al. 2001). Adult *R. luteiventris* have been found to travel up to 5.5 km along high desert streams in Nevada (Reaser 1996), but all other studies have reported dispersal distances <1.3 km (Turner 1960, Hollenbeck 1974, Patla 1997, Bull and Hayes 2001).

Information on juvenile dispersal in this study is difficult to interpret because I did not mark metamorphosing frogs as they emerged from the breeding ponds and recently metamorphosed juveniles remained at the breeding ponds several weeks after all of the adults had migrated to overwintering sites. Most young-of-the-year juvenile frogs still had not migrated to overwintering sites when my field operations ended in late September. However, the presence of juvenile frogs in winter habitats in July suggests that they did complete fall migrations, but much later than adults and older juveniles. In addition, I captured juvenile frogs as far as 350 m from breeding sites, indicating that they disperse from breeding sites. In general, juvenile ranids have been found to disperse further than most adults, traveling from 2 to 5 km from their natal pond (Dole 1971, Berven and Grudzien 1990, Seburn et al. 1997). Information on post-metamorphic dispersal of *R. luteiventris* needs to be addressed with future research.

Migration to Fall/Winter Habitat

Few studies have described amphibian movement patterns to overwintering sites, and consequently, very little is known about the winter habitat requirements of amphibians (Sinsch 1990). My data suggest that *R. luteiventris* show strong site fidelity to a particular overwintering site, even if the migration route is in an opposite direction and over much more difficult terrain than the migration route traveled by other frogs from the same breeding site (as in Figure 7B). One of the best studies of fall migrations to winter habitat is of the Canadian toad (*Bufo hemiophrys*) in northwestern Minnesota. Studies spanning a decade found that toads that had bred in various prairie potholes migrated to the same terrestrial overwintering sites annually (Breckenridge and Tester 1961, Kelleher and Tester 1969). This type of hibernation site selection may be fairly typical in landscapes that offer few suitable overwintering sites.

Rates of Travel

The migration rates of adult *R. luteiventris* in this study were considerably greater than those previously reported for this species and other ranids in the western United States. I report maximum travel rates of up to 160 m/hr and at least 700 m/day by a female *R. luteiventris*. Turner (1960) reported maximum rates of travel of 50-189 m/day for adult *R. luteiventris* in Yellowstone National Park. Adult *R. pipiens* have been found to travel from 40-160 m/day (Dole 1965), while the much larger adult bullfrogs (*R. catesbeiana*) have been reported to travel up to 229 m/day (Raney 1940). My findings demonstrate that the travel rates of ranid frogs may be underestimated, possibly as a result of the traditional techniques used (mark-recapture) and the landscapes studied. Because the spatial arrangement of habitat features in a landscape has a strong influence on movement patterns and dispersal distances, reported movement information may merely reflect characteristics of the local landscape and not the capabilities of the animals (Van Gelder et al. 1986). For example, the fastest migration rate for a ranid frog is that of *Hoplobatrachus occipitalis* (Anura: Ranidae) which will migrate 1.4 km in a single night to reach recently filled ponds in the West African savannah following the first heavy rainfall of the season (Spieler and Linsenmair 1998).

Site fidelity to overwintering sites may reflect the importance and limited availability of this habitat feature for amphibians, particularly those living in northern climates. As most amphibian studies have been conducted during the spring and summer, the effect of winter habitat quality on amphibian population or metapopulation dynamics and persistence has been largely overlooked. In other taxa, the availability and quality of winter habitat has been shown to disproportionately contribute to the carrying capacity of a population (Wallmo et al. 1977). In amphibians, this area of research has yet to be investigated. However, studies have documented high amphibian mortality during winter (Bradford 1983), suggesting that the quality of winter habitat may be a critical component of the stability of amphibian populations.

In Figure 3, winter habitats scored high on Factor 1, represented by deep, rocky lakes with perennially flowing outlets. The only overwintering site that did not group with the others was L3, which scored high on Factor 2, representing warm ponds, with emergent vegetation, and perennially flowing springs or inlets. Site L3 was also >3 m deep and was one of two fishless overwintering sites in Skyhigh Basin (trout occupied 67% of all overwintering sites). Unlike the other overwintering sites, site L3 was used for breeding, was occupied year-round, and contained the vast majority of frogs in the basin. This limited data set suggests that frogs may not be able to successfully overwinter in palustrine habitats subject to anoxia and freezing (Bradford 1983) and thus, where deep fishless sites are unavailable, risk predation by trout in lacustrine habitats (Emery et al. 1972).

Travel Routes

Early accounts of *R. luteiventris* describe numerous frogs occupying high mountain streams (Wright and Wright 1933), suggesting that streams may be important habitats, if only for dispersal. Turner (1960) thought that the majority of *R. luteiventris* movements were restricted to streams or intermittent water courses in the latter part of the summer (fall migration), but he thought that appreciable cross-country movements occurred earlier in the season. In Skyhigh Basin, *R. luteiventris* used mostly terrestrial migratory routes, and often traveled at night or during rain events, but was not restricted to these factors. The capacity to make long annual migrations across different habitats over dry ground may reflect the physical ability of *R. luteiventris* to move quickly and use microclimates to reduce water loss. These traits may be critical to their survival in the harsh high-elevation environment.

The dispersal abilities of *R. luteiventris* show that these animals are capable of colonizing new wetlands, including ephemeral and permanent sites where populations may experience occasional local extirpations. The amount of movement observed, usually via terrestrial migration routes, suggests that introduced trout do not pose a significant barrier to adult dispersal and thus do not decrease connectivity among remaining fishless ponds (the opposite pattern of what Bradford et al. (1993) hypothesized). In support of Bradford's connectivity hypothesis, I did not observe any successful juvenile dispersal, suggesting that introduced trout, or other predators, may prey heavily upon dispersing juvenile frogs. If juvenile frogs are more likely to colonize and breed in a new water body than adults, and trout prey heavily on dispersing juveniles, then the presence of introduced trout in intervening streams may decrease the colonization rate (or recolonization) of upstream and downstream wetlands. Studies that have followed juvenile amphibians through to reproductive age have found that 18-24% of the juveniles dispersed to breed in ponds other than their natal pond, while adults were 100% faithful to the ponds in which they first bred (Gill 1978, Breden 1987, Berven and Grudzien 1990). Dole (1971) recaptured 3 adult male *R. pipiens* >5 km from their natal pond. These data imply that juvenile dispersal may be required for successful recolonization events, but studies of other anurans have found that 15-18.5% of the reproducing adults move among breeding sites (Oldham 1966, Christein and Taylor 1978, Reading et al. 1991). My study suggests that adult dispersal and migration among sites is sufficient to colonize vacant wetlands within at least 1 km of breeding sites.

From a conservation/management perspective, these data suggest that protecting breeding sites for montane populations of *R. luteiventris* is not sufficient protection for the species. In some areas, separate breeding, summer, and winter habitats may all be required for the persistence of *R. luteiventris* populations. Identifying and properly managing these high-elevation habitats requires a better understanding of the local habitat use patterns of frog populations.

Chapter II. Local and Basin-level Effects of Introduced Trout on Amphibians in Historically Fishless Watersheds

ABSTRACT

Introduced trout have often been implicated in the decline of high mountain amphibian populations, but few studies have attempted to understand whether fish stocking also influences the distribution and abundance of amphibians throughout entire mountain basins, including in the remaining fishless lakes. I examined this relationship using the relative abundance of long-toed salamanders (*Ambystoma macrodactylum*) and Columbia spotted frogs (*Rana luteiventris*) in fish-containing and fishless lentic sites in basins with varying levels of historic fish stocking. All lentic waters were surveyed for fish and amphibians in 11 high-elevation basins in the Frank Church - River of No Return Wilderness, Idaho, between 1994 and 1999. I found introduced trout (*Oncorhynchus clarki, O. mykiss, O. m. aguabonita*) in 43 of the 101 sites, representing 90% of the total surface area of lentic water bodies. At the scale of individual water bodies, after accounting for differences in habitat characteristics between fish-containing and fishless sites, the abundance of amphibians at all life stages was significantly lower in lakes with fish. At the basin scale, densities of overwintering life stages of amphibians were lower in the fishless sites of basins where more habitat was occupied by trout. My results suggest that many of the remaining fishless habitats are too shallow to provide suitable breeding or overwintering sites for these amphibians and that current trout distributions may eventually result in the extirpation of amphibian populations from entire landscapes, including sites that remain in a fishless condition.

INTRODUCTION

For over a century, trout and other sport fishes have been introduced into historically fishless, high-elevation lakes in western North America to provide recreational fisheries for backcountry anglers (Bahls 1992). Recent concern over the decline in amphibian populations has led researchers to assess the role of fish stocking in the loss of amphibian populations from high-elevation watersheds. Although several recent studies have documented the negative effects of introduced trout on amphibians at the scale of individual water bodies (Hayes and Jennings 1986, Bradford 1989, Fisher and Shaffer 1996, Bradford et al. 1998), few studies have examined the consequences of introduced fish on amphibian distributions at broader spatial scales (but see Bradford et al. 1993, Knapp and Matthews 2000).

Numerous local-scale studies have documented that, in general, amphibians are less likely to exist and to breed successfully in lakes with predatory, nonnative fish (Bradford 1989, Brönmark and Edenhamn 1994, Braña et al. 1996, Gamradt and Kats 1996, Hecnar and M'Closkey 1997, Bradford et al. 1998, Goodsell and Kats 1999, Knapp and Matthews 2000). In part, amphibian breeding success is lower in sites containing predatory fish, because female amphibians avoid laying their eggs (Resetarits and Wilbur 1989, Kats and Sih 1992, Hopey and Petranka 1994). If egg-laying does take place, fish prey upon the embryonic and larval stages (Hayes and Jennings 1986, Gamradt and Kats 1996, Resetarits 1997, Tyler et al. 1998a,b).

Further, the negative effects of introduced fish on amphibians may be magnified in mountain lakes, as compared to low-elevation waters, because many mountain lakes have less habitat structure (greater exposure to predation), lower productivity (reduced prey resources), and shorter productive periods. At high elevations, amphibians usually require more time to reach metamorphosis than lower elevation conspecifics (Anderson 1967, Licht 1975, Howard and Wallace 1985), increasing their probability of predation during the vulnerable larval period. In some circumstances, larvae may overwinter for several years; thus they are restricted to permanent, deeper bodies of water, most of which now contain fish (Bradford 1989, Knapp and Matthews 2000). Furthermore, postmetamorphic amphibians that over-winter in lentic sites may have to share with fish the few areas that do not freeze or become anoxic beneath surface ice.

The effects of introduced fish at broader spatial scales have not been adequately addressed and, to my knowledge, are restricted to two hypotheses. Bradford et al. (1993) suggested that fish introductions in the Sierra Nevada mountains in California have caused the loss of mountain yellow-legged frog (*Rana muscosa*) populations from entire drainages (including fishless lakes) as a result of fish predation on frogs in stocked lakes and the increased isolation of frog populations in the remaining fishless lakes. In subsequent study in the Sierra Nevada, Knapp and Matthews (2000) suggested that the extirpation of this species from entire drainages could also be the result of fish occupying the most suitable habitats (deep lakes), restricting frogs to marginal habitats where extinction rates are high.

The objective of this study was to evaluate how introduced trout influence the distribution and abundance of amphibians at two spatial scales: individual waterbodies (local scale) and headwater cirques (basin scale). To accomplish this, I first tested the hypothesis that introduced trout have important local effects by comparing amphibian densities in sites with and without trout after controlling for habitat differences between fish-containing and fishless sites. Although the local effects of introduced fish on amphibians have been documented in numerous studies, my study is unique in that I examined the local effects of introduced trout on two amphibian species, the long-toed salamander (*Ambystoma macrodactylum*) and the Columbia spotted frog (*Rana luteiventris*), each of which has a different life history and thus potentially different responses to introduced trout. *Ambystoma macrodactylum* larvae overwinter twice before metamorphosing into terrestrial adults, whereas *R. luteiventris* tadpoles complete their larval stage in a single summer (Pilliod and Fronzuto 2002, Reaser and Pilliod 2002). To evaluate the effects of introduced trout on these amphibian species at the basin scale, I tested the hypothesis that within drainage basins, amphibian densities in fishless sites would decline with increasing levels of trout occupancy.

METHODS

Study Area

Between 1994 and 1999, I repeatedly surveyed all lentic habitats (lakes, ponds, flooded meadows) in a 90 km^2 area of the Bighorn Crags, a region of the Salmon River Mountains along the eastern boundary of the Frank Church - River of No Return Wilderness, Lemhi County, Idaho (Figure 1). The study area encompassed the headwater areas of five major drainages forming tributaries of the Middle Fork and Main Salmon rivers. These drainages contained two to three glacial cirque basins at 2300-2800 m. Each basin contained one to 15 permanent lakes or

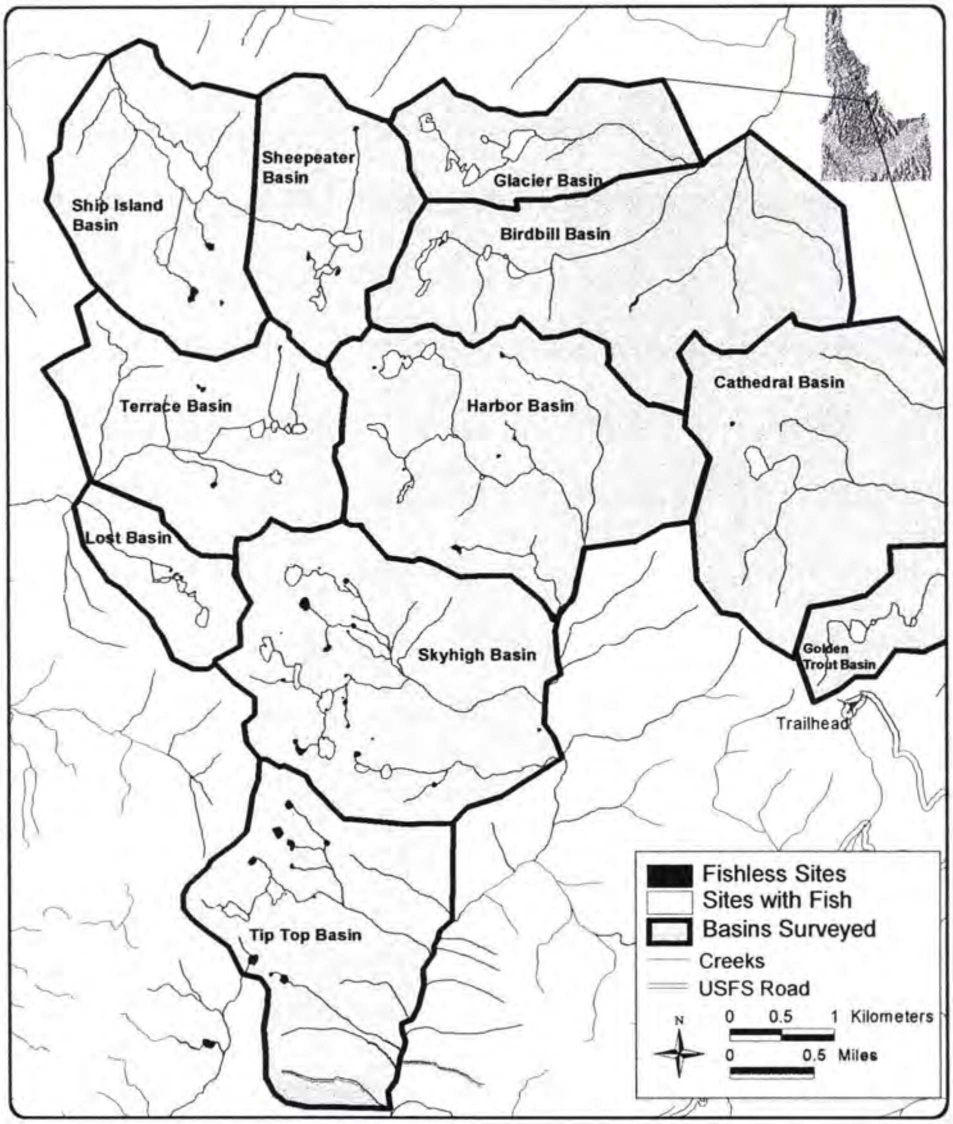


Figure 1. Map of the study area showing the 11 basins studied in the Bighorn Crags, FC-RNR Wilderness, Lemhi County, Idaho. Fishless lakes are shown in black and fish-containing sites are shown in white.

ponds and up to 10 ephemeral ponds and flooded meadows. The basins were separated from each other by headwall ridges of 500-1000 m and steep, cascading outlets dropping 500 to 1000 m into drainage tributaries. In total, I surveyed all 101 lentic sites in 11 basins, including 74 permanent lakes and ponds, 14 permanently flooded meadows, and 13 ephemeral ponds.

The climate of the study area is typical of the Rocky Mountains: winters are long (8 months) and most precipitation falls as snow (>85% of ~80 cm average annual precipitation; Finklin 1988). The dominant vegetation is subalpine fir (*Abies lasiocarpa*) and grouse whortleberry (*Vaccinium scoparium*), with Engelmann spruce (*Picea engelmanni*), alpine rhododendron (*Rododendrous altiflorum*), and sedges (*Carex* sp.) along riparian areas and shorelines of lakes.

The study area is entirely within federally designated wilderness and is relatively free from most anthropogenic disturbance. The area is 4-32 km from the nearest unpaved road and is accessible only by trail. Some recreational impacts were associated with packstock (e.g., horses, llamas), which were mostly localized around a few lakes. The Environmental Protection Agency and USDA Forest Service report negligible changes in air pollution and water quality in the area since 1985 (Jackson 1996).

Although no biotic surveys were conducted in the study area prior to the initial introduction of fish, steep creek gradients (>17% slope) and falls (>3 m) draining each of the basins probably prevented colonizing trout from reaching the headwater lakes (Adams 1999). Therefore, I assumed that all basins were historically fishless (Bahls 1992).

Fish Surveys

I used historical records, hook-and-line angling, gill netting, and visual observations to determine the presence of fish. State stocking ledgers were searched back to 1913, the first year for which written records are available. In 1937 and 1938, the Idaho Department of Fish and Game stocked 60,100 cutthroat trout (*Oncorhynchus clarki*) and rainbow trout (*Oncorhynchus mykiss*) into 12 to 30 previously fishless lakes in the study area to create recreational fisheries (Idaho Department of Fish and Game, unpublished fish stocking records). Although a few lakes were again stocked in the 1950s, regular fish stocking did not begin until the mid 1960s when fish were restocked every 3 to 6 years. In total, more than 300,000 fry or fingerlings have been introduced into 37 lakes. Each of these lakes has been stocked from 4 to 12 times and at least twice since 1989.

To determine the presence of fish, all small ponds and ephemeral pools <1.5 m deep were visually inspected for fish from shore and while wading (N=31). For water bodies >1.5 m deep, I noted the presence of fish during amphibian surveys (N=43). If fish were not observed, I further assessed fish presence/absence using overnight gill net sets (40 by 1.8 m, 7-panels of 10-38 mm mesh) for 12-16 hours (N=11) or snorkeling (N=8), and multiple visual surveys in smaller water bodies (N=8).

Amphibian Surveys

The distribution and abundance of amphibians in all lentic habitats in each basin were determined using visual encounter surveys as described by Crump and Scott (1994) and Thoms et al. (1997). The earliest surveys were conducted during 1-7 July , approximately 1 week after ice-out on the larger lakes (breeding usually occurred in late June to early July). All sites were surveyed in July and August between 1000 and 1700 hours when air temperatures were above 10°C. Nearly all sites were surveyed each year, and some sites were surveyed two to three times each year between 1994 and 1999 (median, 4 surveys/site; range, one to 30).

In each of the 11 basins, teams of two trained observers searched the entire perimeter of each lake and pond (2 m of the littoral zone and 2 m of the riparian zone) and flooded areas of meadows. I enumerated each amphibian life stage both from shore and while wading 1 m from the shoreline. In addition, dip nets were used to sweep the substrate and, when present, the aquatic vegetation. I calculated amphibian densities as the maximum number of individuals observed at each site/area searched (m^2). Larval salamanders <25 mm snout-vent length (SVL) were considered to be in their first year and larvae >26 mm SVL were considered to be 2 or more years old (Anderson 1967). Salamander larvae transformed in July of their 3rd year (at ~36-48 mm SVL). Too few adult *A. macrodactylum* were captured to reliably estimate population size so I did not analyze adult salamander abundance. Juvenile frogs were defined as postmetamorphic frogs that had overwintered at least once and were <46 mm SVL (Turner 1960). I did not include young-of-the-year post-metamorphic frogs in any analyses because relatively few surveys were conducted in late September when recently metamorphosed frogs could be counted.

To evaluate how accurately my visual surveys estimated the abundance of amphibians, I compared visual salamander counts made while wading to counts made using snorkel surveys in 11 lakes and compared visual frog counts with Lincoln-Petersen mark-recapture population estimates in 39 lakes. Salamander counts made using visual surveys were comparable to salamander counts made during snorkel surveys (N=11, Pearson r^2=0.90, *P*<0.001; B. Hoffman and D.S. Pilliod, unpublished data) and visual survey frog counts were comparable to population estimates (N=39, Pearson r^2=0.96, *P*<0.001).

Site Descriptions

I used a combination of field and laboratory measurements to quantify the physical, chemical, and biological characteristics of each lentic wetland. Surface area, perimeter, and elevation were obtained from 1:24,000 topographic maps or a geographic information system (GIS). Maximum depth was measured with a tape measure or hand-held sonar gun. Conductivity and pH were measured at the outlet of each site using Oakton hand-held meters (models T3, pH2). Water temperature was recorded at the beginning of each survey (at 5 cm deep and within 1 m from shore) and then averaged within and among years. I estimated the relative amounts of aquatic littoral and terrestrial riparian substrate subclasses along the shoreline or over the area of each site (modified lacustrine and palustrine system classification, National Wetland Inventory; Cowardin et al. 1979). Terrestrial substrate subclasses included forest, shrub, forb-graminoid, rock, and woody debris. Aquatic subclasses included bedrock, cobble-gravel, silt/organic mud, vegetation, and woody debris. I calculated the proportion of shoreline made up of each substrate class by summing the linear distances of each class around a site and dividing by the site perimeter.

Statistical Analyses

To evaluate the local effects of introduced trout on amphibian populations, I first compared amphibian densities in sites with and without fish using a Mann-Whitney U test (Sokal and Rohlf 1995). I did not use parametric models, even with transformed variables, because the data were skewed by the low densities of amphibians in fish-containing sites.

To minimize the potentially confounding influence of habitat differences between sites with and without fish, I used a two-step approach. First, to determine which habitat variables were associated with fish-containing sites, I entered all habitat variables into a backward stepwise logistic regression. I then used the resulting model to select those fishless sites that had similar values for significant habitat variables as sites with fish. This model identified 10 fishless sites that were very similar in habitat characteristics to fish-containing sites (N=43). This subset of fishless sites was used to evaluate the effects of fish on amphibian densities while minimizing the habitat differences between fish-containing and fishless sites. Amphibian densities in these two types of sites were compared using a Mann-Whitney U test. I used this approach instead of multiple regression because my dependent variables, amphibian densities, were always nonnormal due to many sites that lacked amphibians. These skewed distributions could not be normalized using standard transformations.

To further evaluate whether *A. macrodactylum* and *R. luteiventris* used deep lakes (≥2 m) for breeding and to determine whether amphibian reproduction in deep lakes was successful, I compared the densities of first-year and second-year amphibian life stages among fishless sites as a function of maximum lake depth (<2 m, 2-4 m, 4-6 m, ≥6 m) using chi-square approximations of the Kruskal-Wallis test (Sokal and Rohlf 1995). To determine possible landscape effects of introduced trout on amphibian abundance at the basin scale, I performed simple linear regression analyses on the mean density of amphibians in fishless sites as a function of the percent area of lentic habitat containing trout in a basin. The influence of outliers was assessed with the F approximation of Cook's distance (Ramsey and Schafer 1997).

To differentiate between the effects of fish and the effects of differences in habitat among basins, I first reduced the number of habitat variables using factor analysis with a principal component extraction and varimax rotation. Factor scores were calculated for each site. I then evaluated the significance of differences in the average factor scores among basins using multivariate analysis of variance (MANOVA), with factor scores as my dependent variables and basin as my independent variable. These models met assumptions of normality and homoscedasticity but not equality of covariance matrices. Therefore, I evaluated model significance using Pillai's trace, a conservative and robust multivariate F test (Norusis 1990). To identify which factors were significantly different among basins, I performed multiple univariate analysis of variance (ANOVA), again using factor score as my dependent variable and basin as my independent variable. Finally, to determine which basins were significantly different from each other, I used Tukey's pair-wise comparisons on each of the significant factors. Similarly, to determine whether fishless sites had significantly different habitat among basins, I repeated the above procedure, but only included factor scores from fishless sites.

In regression analyses and MANOVAs, I screened predictor variables for colinearity and excluded redundant variables from analyses. These included area and perimeter, which were correlated with depth, and woody debris and bedrock, due to the redundancy of including all subclasses in percentage estimates. Conductivity also was excluded because there was little variation across sites (mean, 5.5 μS; range, 0-30 μS). I performed all analyses on SPSS software v.10.0 (SPSS Inc, Chicago, IL) and used $\alpha=0.05$ as a significance criterion.

RESULTS

Introduced cutthroat, rainbow, or golden trout and their hybrids were found in all basins, but the percent of sites and area of habitat occupied by trout varied among basins (Table 1 and Figure 1). I found trout in 43% of all lentic sites, accounting for 90% of the available surface area of lentic habitat. Trout occupied the majority of lakes that were 1 or more ha in surface area and deeper than 4 m, while most sites <1 ha in surface area and <4 m deep were fishless (Figure 2). As a result, the more lentic habitat that was occupied by trout in a basin, the fewer deep, fishless sites remained (Table 1). Only two basins, Skyhigh and Tip Top, had <90% of the surface area of their lentic habitat occupied by trout, and both of these basins contained several deep, fishless lakes that presumably could have supported trout populations. Other basins contained at most one deep, fishless lake (Table 1).

Table 1. Summary of the total number of lentic waterbodies, the number of waterbodies with fish, the percent of waterbodies with fish, the total surface area of lentic waterbodies, and percent surface area occupied by fish in 11 basins in the Bighorn Crags of the Frank Churck-River of No Return Wilderness, Idaho.

Basin	Total # Sites	Total # Sites with Fish	Percent Sites with Fish (%)	Total Surface Area Sites (ha)	% Surface Area Fish Present
Birdbill	9	5	56	7.17	95.8
Cathedral	2	1	50	7.25	99.7
Glacier	7	7	100	16.87	100.0
Golden Trout	3	3	100	5.29	100.0
Harbor	12	4	33	15.38	92.2
Lost	6	4	67	5.14	98.1
Sheepeater	5	3	60	11.11	95.7
Ship Island	5	2	40	43.75	95.7
Skyhigh	29	7	24	24.75	81.1
Terrace	7	5	71	7.63	95.5
Tip Top	16	2	13	14.43	52.5
Totals	**101**	**43**	**42.6**	**158.8**	**90.0**

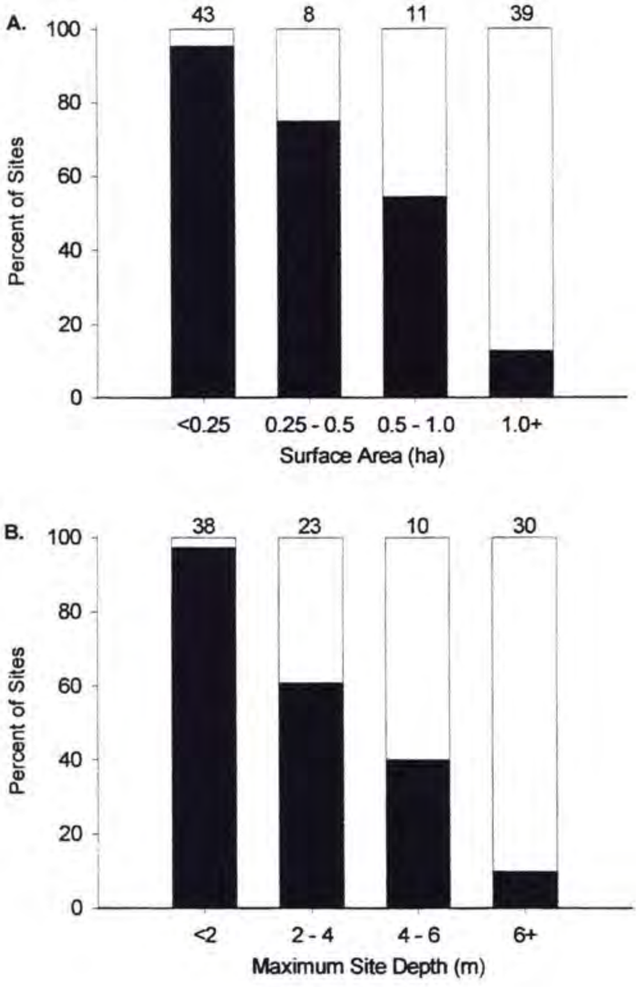


Figure 2. Frequency histograms showing the proportion of fishless (black) and fish-containing (white) lentic sites as a function of surface area (A) and maximum lake depth (B) in the Bighorn Crags of the Frank Church River of No Return Wilderness. Numbers above bars indicate the number of sites in each category.

Local-scale Effects of Introduced Trout on Amphibians

The densities of all life stages of *A. macrodactylum* and *R. luteiventris* were significantly lower in fish-containing sites than in fishless sites (for all life stages; N=101, U=647-930, $P \leq 0.018$; Figure 3). The logistic regression analysis used to identify fishless sites that had similar habitat as fish-containing sites was significant (df=2, $\chi^2=58.50$, $P<0.001$, $r^2=0.59$). Greater maximum depths and rocky substrates characterized lakes with fish. Fishless sites selected using the logistic regression model were also deep, rocky lakes. Comparisons between these 10 fishless sites and the 43 sites where fish occurred indicated that fish-containing sites again had significantly lower densities of all life stages of amphibians than did fishless sites with similar habitat (for all life stages; N=53, U=48-86, $P \leq 0.002$).

Basin-scale Effects of Introduced Trout on Amphibians

Ambystoma macrodactylum and *Rana luteiventris* reproduced in lentic sites ranging in depth from 0.2 to 6 or more m and the densities of first-year salamander larvae and frog tadpoles were not significantly different among fishless sites across this range of depths (1st yr *A. macrodactylum* larvae: df=3, $\chi^2=3.2$, $P=0.36$, Figure 4A; *R. luteiventris* tadpoles: df=3, $\chi^2=6.3$, $P=0.10$, Figure 4B). However, among these fishless sites, densities of amphibian life stages that had overwintered at least once were significantly lower in sites <2 m deep than in deeper sites (2nd yr *A. macrodactylum* larvae: df=3, $\chi^2=24.2$, $P<0.001$, Figure 4A; juvenile *R. luteiventris*: df=3, $\chi^2=9.3$, $P=0.025$, Figure 4B).

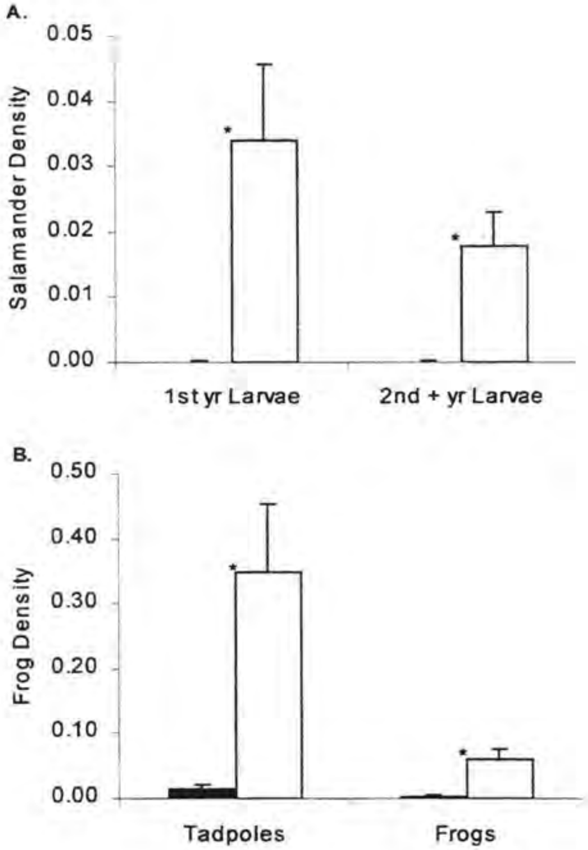


Figure 3. Mean density (# per m^2 searched; + 1 SE) of first and second-year salamander larvae (A) and spotted frog tadpoles and juveniles + adults (B) in sites with (black bars) and without introduced trout (white bars) in the Bighorn Crags of the FC-RNR Wilderness between 1994 and 1999. Asterices between pairs of bars indicate that the densities of all life stages of amphibians were significantly lower in lakes with fish compared to fishless sites (*P<0.001).

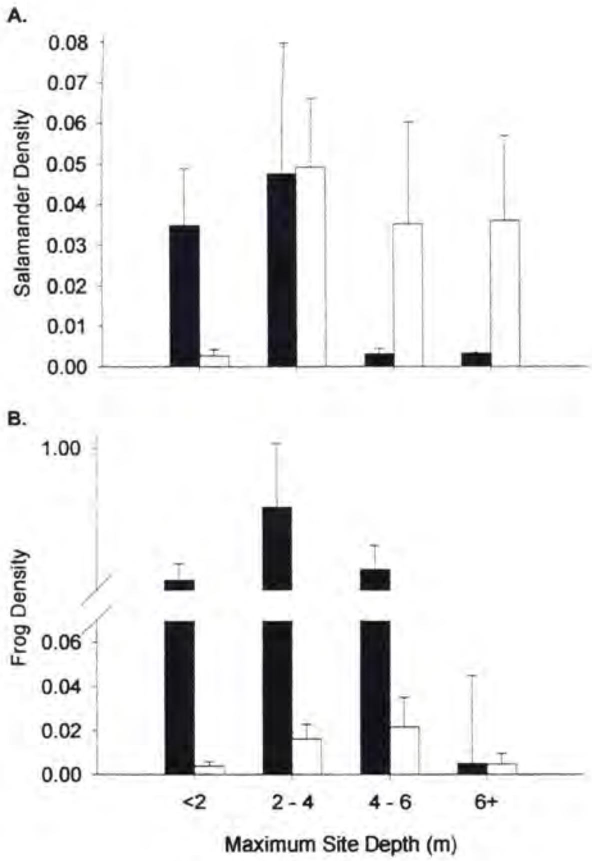


Figure 4. Mean density (# per m^2 searched; + 1 SE) of first (black bars) and second-year (white bars) salamander larvae (A) and spotted frog tadpoles (black bars) and juveniles + adults (white bars) (B) in fishless sites as a function of the maximum depth of each site in the Bighorn Crags of the FC-RNR Wilderness between 1994 and 1999. First-year larvae and tadpoles were abundant in shallow sites (<2 m deep) while densities of older life stages were lowest in sites <2 m.

Among basins, the density of first-year amphibian life stages in fishless sites was not related to the percent surface area of lentic sites occupied by trout (Figures 5A and 6A). However, the percent surface area of lentic sites occupied by trout was a highly significant predictor of the density of salamander larvae at least 2 years old in fishless sites (Adj. $R^2=0.95$, $F_{1,7}=167.4$, $P<0.001$; Figure 5B) and of the density of adult and juvenile frogs in fishless sites (Adj. $R^2=0.98$, $F_{1,7}=330.7$, $P<0.001$; Figure 6B). Both of these relationships were strongly influenced by the data point for Tip Top Basin (lentic surface area containing fish = 52%), as measured by the F approximation to Cook's distance. When I excluded this data point from the models, no other basins had a disproportionate influence on the regression and the linear regression was still highly significant for both salamanders (Adj. $R^2=0.64$, $F_{1,6}=13.4$, $P=0.011$; Figure 5B) and frogs (Adj. $R^2=0.81$, $F_{1,6}=31.47$, $P=0.001$; Figure 6B). Therefore, densities of older amphibian life stages in fishless sites decreased with increases in the proportion of lentic habitat occupied by trout.

Habitat characteristics of all sites formed five composite factors, three of which were significantly different among basins (Pillai's trace=0.83, $F_{50,450}=2.0$, $P=0.001$). These three significant factors characterized lakes with (1) greater rocky substrate, (2) sparse aquatic vegetation and at higher elevations, and (3) greater maximum depths and forested shorelines. Pair-wise comparisons indicated that Glacier Basin had significantly higher factor scores than Tip Top Basin for the factor that characterized lakes with sparse aquatic vegetation at higher elevations. No other factors were significantly different among individual basins. Habitat characteristics of fishless sites were not significantly different among basins based on composite factor scores (Pillai's trace=0.69, $F_{35,245}=1.12$, $P=0.31$). Therefore, the relationships between amphibian density in fishless sites and percent of lentic surface area occupied by trout (Figures 5 and 6) were unlikely to have been confounded by habitat differences among basins.

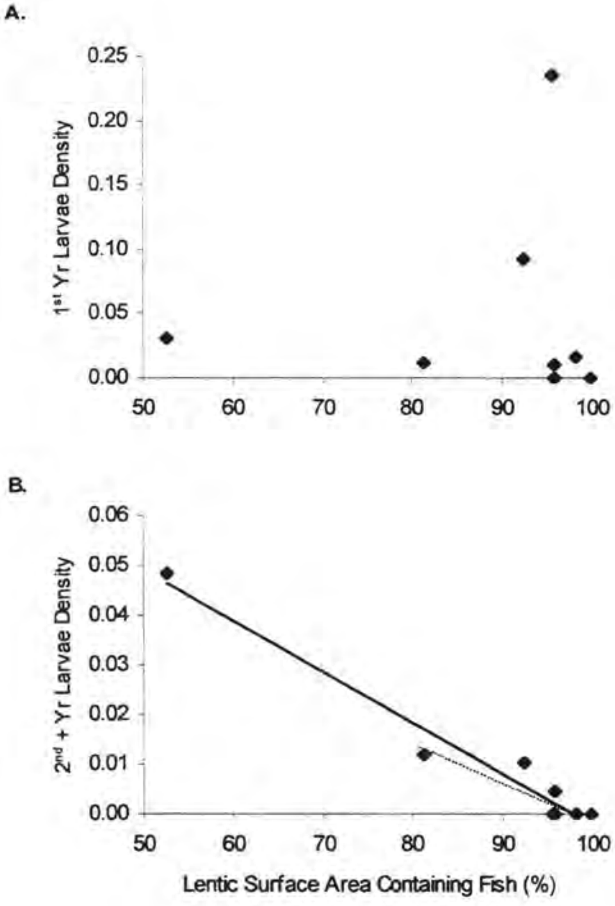


Figure 5. Plot of the relationship between the percentage of lentic water surface area containing trout in a basin and the mean site density (# per m^2 searched) per basin of first-year long-toed salamander larvae (A) and second-year long-toed salamander larvae (B) in fishless sites in the Bighorn Crags of the Frank Church-River of No Return Wilderness. Each point is a basin. Significant linear regression lines are shown. The Tip Top Basin data point is an outlier in this model, but the relationship remained highly significant when this data point was excluded. The linear regression line without the outlier is shown as a dashed line.

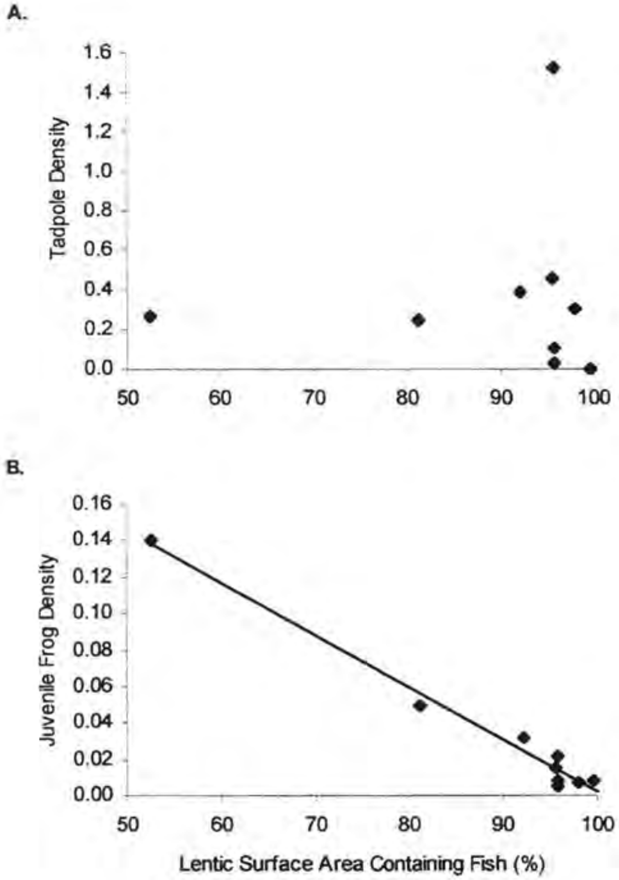


Figure 6. Plot of the relationship between the percentage of lentic water surface area containing trout in a basin and the mean site density (# per m^2 searched) per basin of spotted frog tadpoles (A), and juveniles + adults (B) in fishless sites in the Bighorn Crags of the Frank Church-River of No Return Wilderness. Each point is a basin. Significant linear regression lines are shown.

DISCUSSION

Recent studies have documented the negative local effects of introduced trout on amphibian abundance and occurrence in high mountain lakes in the western United States (Bradford 1989, Bradford et al. 1998, Tyler et al. 1998a, Knapp and Matthews 2000). This study is unique in that I also examined whether the negative effects in stocked lakes have implications for the distributions of these amphibians across a landscape (that is, whether impacts extend to fishless sites in a basin) and did so by studying two amphibians with very different life histories. This information is needed to explain the reported declines and extirpation of high mountain amphibians from landscapes (basins, watersheds) where fishless habitats still exist (e.g., Fellers and Drost 1993, Bradford et al. 1994, Drost and Fellers 1996, Knapp and Matthews 2000).

In congruence with other studies, I found that the abundance of all life stages of *A. macrodactylum* and *R. luteiventris* was lower in sites with fish than it was in fishless sites (Tyler et al. 1998a, Knapp and Matthews 2000). However, without pre-stocking records with which to compare current amphibian densities, I cannot be certain whether amphibian populations at fish-containing sites are smaller now than they were before trout were introduced. A common argument is that sites now occupied by trout are, and always were, poor habitat for amphibians because these sites are typically deep, rocky lakes. However, few studies have examined the habitat associations and requirements of high-elevation amphibians; thus, this perception has little scientific basis. I found significantly larger populations of amphibians in fishless than in fish-containing sites, even after accounting for the differences in habitat; this suggests that *A. macrodactylum* and *R. luteiventris* may historically have had large populations in lakes now occupied by trout. Based on the low abundance and recruitment of amphibians in lakes with fish, I suspect that lakes with fish are sink populations for amphibians where juvenile recruitment insufficiently compensates for adult mortality (Pulliam 1988, Pulliam and Danielson 1991). Local extinction of amphibian populations at such sites may be prevented by the immigration of juveniles and adults from nearby fishless sites that frequently act as sources.

Despite relatively high levels of reproduction in fishless sites <2 m deep (as seen in Figure 4), I rarely found second-year salamander larvae and juvenile frogs in these shallow ponds, suggesting that both species generally require lentic sites at least 2 m deep for surviving through winter. In shallow ponds, *A. macrodactylum* larvae risk desiccation during summer and freezing or anoxic conditions during winter (I occasionally found dead larvae in these shallow sites during spring surveys), whereas in deep lakes they risk predation from introduced trout. Because high-elevation populations of *A. macrodactylum* have a long larval stage (2 - 3 years)(Anderson 1967), they may be more restricted to deeper waterbodies and thus have lost most of their suitable breeding habitat to introduced fish. Mountain yellow-legged frogs, endemic to the Sierra Nevada, also have multiple-year larval stages. Recent research suggests that the loss of deep, fishless breeding sites is threatening the persistence of this species across its range (Knapp and Matthews 2000).

In contrast to salamanders, *R. luteiventris* are able to breed successfully in shallow, fishless sites, because most of the tadpoles transform into juveniles before the lakes begin to freeze. I did not observe any overwintering tadpoles, a finding consistent with the life history of this species across its range. In the late summer, recently metamorphosed juveniles migrated with adults and older juveniles to deeper bodies of water to overwinter (see Chapter I). Based on my observations indicating that the highest overwinter survival of postmetamorphic frogs occurred in deeper, fishless sites, I suggest that predation by trout on juveniles that migrated from shallow fishless sites to deep, fish-containing lakes may effectively eliminate successful reproduction at fishless sites. Because trout now occupy 67% of all lentic sites ≥ 2 m deep in the study area, the majority of high-quality overwintering habitat for these amphibians has been lost.

The overwintering requirements of *A. macrodactylum* larvae and *R. luteiventris* may provide a mechanism that would explain why the local-scale negative effects of introduced trout can extend to an entire basin. Basins with more lentic habitat occupied by introduced trout had fewer deep, fishless sites and lower densities of late-stage salamander larvae and postmetamorphic frogs (>1 yr old) in fishless sites. Because first-year salamander larvae and frog tadpoles were fairly abundant in fishless sites in all basins, the low density of older life stages of these amphibians in fishless sites in heavily stocked basins was likely due to lower survival in basins that lacked sufficient deep, fishless habitat.

The combined negative effects of introduced trout at local and basin scales demonstrated by this study may have consequences for amphibian persistence within the study basins. Now mostly occupied by trout, deep lentic habitats in the study area likely provided critical breeding and winter habitat for salamanders and frogs and thus may have been important amphibian source populations in many basins prior to fish introductions. I believe that the shallow water bodies that make up the majority of remaining fishless habitat may be sink habitats for amphibians. Although the amphibian populations at these sites may have been maintained by immigration from source populations prior to fish introductions, most of these source populations have been extirpated by the introduced trout. In the absence of immigration, I expect these populations to eventually disappear.

Based on the negative effects of trout on amphibians in fish and fishless sites, what evidence do I have that this condition may be threatening amphibian persistence? *A. macrodactylum* may have already disappeared from three of 11 basins (Cathedral, Ship Island, Sheepeater), including an entire drainage, and they appear to be on the verge of extirpation in several other basins (Glacier, Golden Trout, Lost). I cannot be certain that salamanders historically inhabited the three basins in which they are currently absent, but the wide distribution of this species and characteristics of the habitat in these basins indicate that they most likely once supported salamander populations. *A. macrodactylum* populations may be particularly vulnerable to extinction following trout introductions because they are generally highly philopatric, have relatively small home ranges (less than 300 m^2), and may only disperse up to 100 m away from breeding sites (Sheppard 1977, Beneski et al. 1986, Powell et al. 1997).

Despite the local- and basin-scale effects of introduced trout on *R. luteiventris*, this species still occurred at almost all sites and in all basins in this study area. Several studies have concluded that local populations of lentic-breeding amphibians may be able to persist in sink habitats due to relatively high immigration and the "rescue effect" associated with some metapopulations (Gill 1978, Sjögren 1991, Gibbs 1993, Sjögren-Gulve 1994, Sinsch 1992, 1997). However, these results also suggest that *R. luteiventris* may be more threatened than their widespread distribution indicates. Tadpole survival, juvenile recruitment, and the abundance of frogs in most of the heavily stocked basins were lower than in basins with less habitat occupied by trout. In addition, the age structure of frogs in fish-dominated basins indicates that the frogs have not reproduced successfully for 6 to 8 years. Given the longevity of these animals (12-14 years)(Turner 1960), *R. luteiventris* may soon disappear from the basins where remaining fishless sites do not provide adequate overwintering habitat.

A question that is often asked is, why have fish not eliminated these amphibians sooner? Based on the evidence in this study and others, I believe that the initial local impacts of fish introductions occurred within years (Terrero 1951, Macan 1966, Sexton and Phillips 1986, Aronsson and Stenson 1998, Meyer et al. 1998), but that the extirpation of amphibians at broader spatial scales took many decades (Bradford et al. 1993, Knapp and Matthews 2000). Frogs and salamanders were probably once widely distributed and were quickly eliminated - or nearly eliminated - from lakes where trout were introduced. The quality of the remaining fishless habitats may have been insufficient to maintain viable populations, and remaining populations are probably continuing to decline slowly. Because the lakes in this study were not regularly stocked until the 1960s, these amphibians have only experienced high trout densities for a relatively short time (40 years or only about four generations). Factors such as metapopulation dynamics can prolong declines to extinction, especially among long-lived organisms like high-elevation amphibians (Sjögren 1991, Hanski 1997).

Restoration

Conserving natural biodiversity and maintaining functioning ecosystems is a goal of protected area management. The results of this study suggest that wildlife managers need to consider restoring a few deep lakes in each basin to create fishless breeding and overwintering habitat for amphibians (Knapp 1996, Knapp and Matthews 1998, Pilliod and Peterson 2000). Given that some amphibian reproduction is occurring, even in heavily stocked basins (see Figures 5A and 6A), I suspect that amphibian populations could recover quickly if a few deep lakes were restored to a fishless state (Brönmark and Edenhamn 1994, Knapp 1996, Funk and Dunlap 1999, Knapp et al. 2001). However, because amphibian populations in mountain basins are widely isolated from each other (Howard and Wallace 1981, Call 1997, Tallmon et al. 2000), recolonization following the extirpation of amphibians from entire basins could take decades.

Chapter III. The Influence of Landscape Structure on Amphibian Population Dynamics: A Test of Dunning's Hypotheses

ABSTRACT

Numerous studies have examined the influence of local habitat conditions on animal populations, but only in the last decade or so have ecologists broadened their focus to assess the influence of landscape structure on animal population dynamics. To provide a framework for evaluating the different ways the landscape can influence population dynamics, Dunning et al. (1992) proposed several "ecological processes" or landscape effects, which included landscape complementation, landscape supplementation, source-sink relationships, and neighborhood effects. All of these landscape effects highlight the influence of surrounding habitat patches on individual populations. Landscape complementation and supplementation are measures of the proximity and utilization of important resources to a population, whereas source-sink and neighborhood relationships deal with the influence of populations on each other through immigration and emigration. To investigate the relative influence of local habitat conditions and different landscape effects on population size, I used data from a 4-year field study on montane Columbia spotted frog (*Rana luteiventris*) populations in central Idaho. Both local and landscape factors had significant effects on frog abundance. *Rana luteiventris* abundance decreased with increasing distance from breeding sites to the nearest overwintering site (complementation). The largest *R. luteiventris* population had >25 % of the female population migrating to surrounding wetlands to forage, resulting in significantly larger female frogs returning in the fall compared to resident females. By supplementing their food resources elsewhere, migrating females likely reduced competition at the breeding

site and grew larger; migrating females may have been able to contribute more offspring to the population. This combination of factors appears to enable a population to be larger than could be supported by local resources. *R. luteiventris* abundance was more strongly influenced by the area of fishless habitat nearby, than by the total area of habitat (neighborhood effects). The probability of occupancy of population sinks decreased with increasing distance from the nearest source and the abundance of frog populations in population sinks decreased with increasing distance from the nearest breeding site. These results suggest that amphibian populations can be influenced by landscape structure and warrant further investigations. Given these results, I recommend that conservation efforts to protect amphibian populations consider the spatial arrangement of aquatic and terrestrial habitats and the proximity of populations in a drainage or region.

INTRODUCTION

Understanding why a species is abundant in some locations and not in others, has been a central problem in ecology (Brown 1984). The traditional approach has been to compare the quality of habitat patches in terms of local abiotic (substrate, temperature, moisture) and biotic (vegetation, food resources, predators) conditions. However, increasing human uses of land (e.g., urban sprawl, agriculture, roads) have resulted in broad-scale habitat alteration and fragmentation (Saunders et al. 1991, Meyer and Turner 1994), which has shifted the focus of ecological studies to include the influences of landscape structure on local population dynamics (Fahrig and Paloheimo 1988). Understanding how animal populations will respond to changes in the distribution of suitable habitats is one of the primary concerns in conservation biology. However, scientists have only recently begun to investigate the effects of landscape structure on animal population dynamics and persistence (Turner and Gardner 1991, Wiens 1997).

In 1992, a group of scientists from the University of Georgia published a particularly thought-provoking, but seemingly overlooked paper (Dunning et al. 1992), which provided a framework for understanding the effects of the landscape on animal populations. The authors identified several landscape effects (=Dunning's ecological processes) that could potentially influence animal populations above and beyond local habitat characteristics. Because "processes" in ecology generally refer to dynamic functions such as energy flow and nutrient cycling, I prefer to call these concepts "landscape effects". Dunning et al.'s (1992) landscape effects included (1) landscape complementation or the utilization of spatially separated non-substitutable resources, such as breeding sites and hibernacula, (2) landscape supplementation or the utilization of spatially separated substitutable resources such as foraging areas, and (3) neighborhood effects or the idea that population abundance in a particular patch may be more strongly affected by characteristics of nearby patches than by local habitat characteristics (Table 1). Dunning et al. (1992) also discuss source/sink relationships, but I incorporated this discussion into neighborhood effects.

Table 1. List of landscape effects that Dunning et al. (1992) used to describe the influence of the landscape on population dynamics. I have provided definitions for each landscape effect and the specific hypothesis tested in this paper.

Landscape Effects	**Definitions**	**Hypotheses**
Landscape Complementation	Utilization of spatially separated non-substitutable resources (e.g., breeding sites and hibernacula)	1. Sites closer to complementary resources will support more individuals than sites further from complementary resources.
Landscape Supplementation	Utilization of spatially separated substitutable resources (e.g., foraging patches)	2. Populations that are able to supplement their resources at adjacent sites will have larger populations than can be supported by their local patch.
Neighborhood Effects	Population abundance in a particular patch may be more strongly affected by characteristics of nearby patches than by local habitat characteristics or than by distant habitat patches.	3. Populations are more likely to be influenced by nearby patches of suitable habitat than distant or less suitable habitat patches.

For each of these landscape effects, the authors proposed several hypotheses that predict how animal populations might respond to the distribution and acquisition of resources in the environment. The authors provided a few empirical studies that supported some of these hypotheses, but since this publication, relatively few studies have further tested these hypotheses. In this paper, I first evaluate the relationship between local habitat conditions and population size and then assess the influence of different landscape effects on population size within Dunning et al.'s (1992) framework (Table 2).

Table 2. Summary of dependent and independent variables used in this study to evaluate the influence of various determinants of local population size.

Determinant	Dependent Variable	Independent Variable
1. Local Habitat Condition	# frogs per water body	elevation, surface area, max. depth, etc. (Table 3)
2. Landscape Context		
a. Complementation	a. # frogs per water body	a. distance from breeding site to overwintering site
b. Supplementation	b. # frogs per water body	b. supplement vs. non-supplementing populations
c. Neighborhood Effects	c. # frogs per water body	c. area of suitable habitat within 1000 m
3. Temporal Context		
a. Seasonal Distribution	a. Part of landscape complementation	
b. Annual Fluctuation	b. Not addressed in this study but an important part of metapopulation dynamics	

Landscape structure is loosely defined as the spatial relationships among various habitats in a heterogeneous landscape, which can be thought of as having three components (Turner 1989). Dunning et al. (1992) described landscape structure in terms of composition (relative amounts of various habitats) and physiognomy (spatial arrangement of habitats). Taylor et al. (1993) added that the ability of an organism to acquire its resources in a heterogeneous environment depends not only on the distance to its resource patches, but also its ability to get there. They argue that connectivity, or the degree to which landscapes facilitate or impede animal movements among habitats, is a critical measure of landscape structure that may influence animal population dynamics. Although each of these three components of landscape structure (landscape composition, landscape physiognomy, and landscape connectivity) is important, for this paper, I only examine the influence of distance between resource patches. Therefore, my tests of Dunning et al.'s hypotheses focus on landscape physiognomy and use a simplistic spatial model, which only considers resources distributed in suitable habitat patches surrounded by unsuitable habitat matrix. The limitations of this approach are discussed and other approaches suggested.

I examined several of the central hypotheses proposed by Dunning et al. (1992) in relation to the population structure and dynamics of Columbia spotted frogs (*Rana luteiventris*) in a heterogeneous montane landscape in central Idaho. The specific hypotheses that I test in this paper are: (1) sites closer to complementary resources will support more individuals than sites further from complementary resources, (2) populations that are able to supplement their resources at adjacent sites will have larger populations than can be supported by local patch resources, and (3) populations are more likely to be influenced by nearby patches of suitable habitat than by distant or less suitable habitat patches (Table 1). *R. luteiventris* is an appropriate taxon to test these hypotheses because they often exist in subpopulations which are closely tied to distinct habitat patches (specific breeding ponds), but may also require different habitats for overwintering and foraging (e.g., lakes, streams, meadows, uplands).

METHODS

Study Area

The study area encompassed a 90 km^2 area known as the Bighorn Crags in the Salmon River Mountains along the eastern boundary of the Frank Church - River of No Return Wilderness, Lemhi County, Idaho (Figure 1). This paper focuses on the distribution and abundance of *R. luteiventris* in 101 lentic habitats (lakes, ponds, flooded meadows) distributed across 11 glacial cirque basins at 2300-2800 m elevation. Some of the results are specific to Skyhigh Basin at about 2600 m in elevation. For a detailed description of Skyhigh Basin and of the overall study area, see chapters I and II, respectively.

Frog Surveys and Monitoring

Between 1995 and 1998, I surveyed all lentic wetlands and associated lotic habitats in the study area for *R. luteiventris* using visual encounter methodology (Thoms et al. 1997). Most wetlands were surveyed at least once per year (median = 4

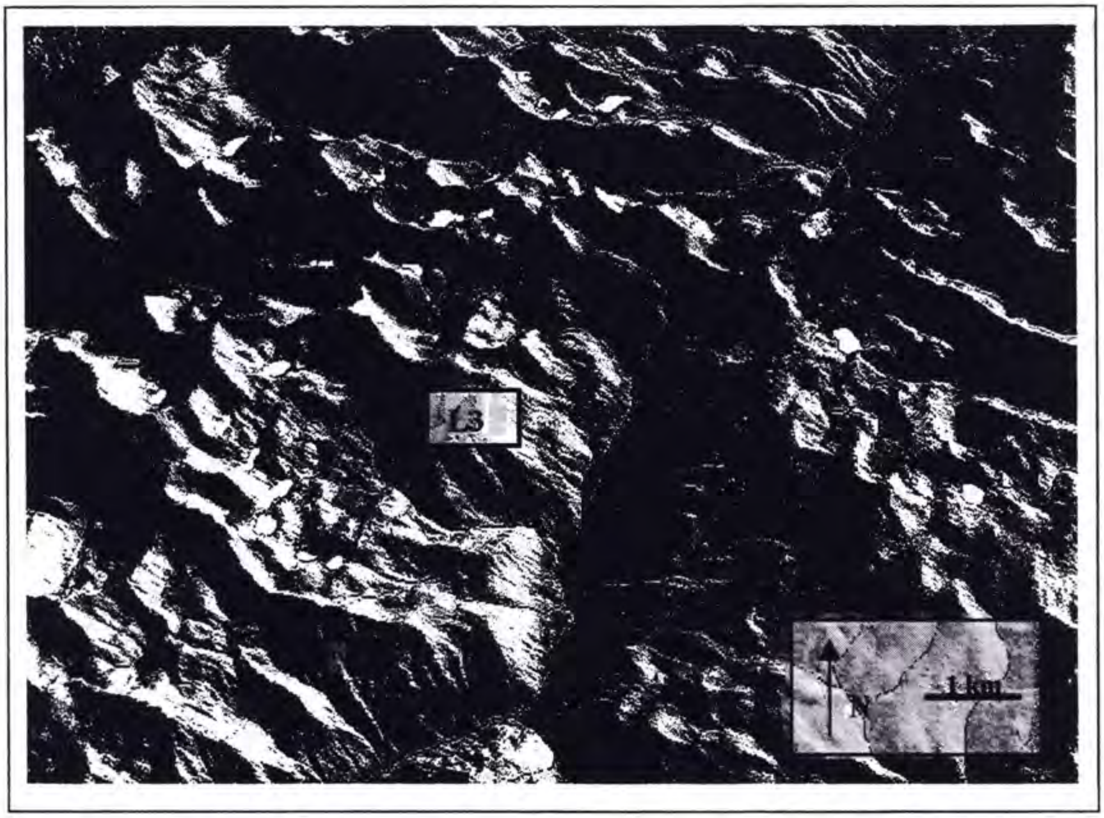


Figure 1. Digital elevation model of the study area in the Bighorn Crags, Frank Church-River of No Return Wilderness, Lemhi County, Idaho. All palustrine and lacustrine wetlands are shown. Black wetlands are *R. luteiventris* breeding sites. White wetlands are non-breeding sites, most of which were occupied by *R. luteiventris* between 1995 and 1998. Site L3 is labeled.

surveys/site, range 1-30). During surveys, all life stages of *R. luteiventris* were counted. The consistency of relative abundance estimates was verified with repeated within-year surveys and mark-recapture population estimation in 1995. I calculated amphibian densities as the maximum number of individuals observed at each site/area searched. Juvenile frogs were defined as post-metamorphic frogs that had over-wintered at least once and were <46 mm SVL (Turner 1960). I did not include young-of-the-year post-metamorphic frogs in any analyses because relatively few surveys were conducted in late September when recently metamorphosed frogs could be counted. To determine dispersal among sites, I marked all adult and juvenile *R. luteiventris* captured with a site-specific 2-3 digit toe clip.

To document the important habitat features for *R. luteiventris* in a landscape, I intensively studied one basin (Skyhigh) using multiple within- and between-year surveys, and radiotelemetry, from 1995-97 (see chapter I). In Skyhigh Basin, I was able to identify most breeding, summer, and winter habitats for *R. luteiventris.* This basin provided tests of population abundance in relation to distance from overwintering sites, as well as insights into landscape complementation, landscape supplementation, and source-sink relationships.

In this paper, I loosely used the "ponds-as-patches" approach to landscape structure (Marsh and Trenham 2001), although some palustrine wetlands were flooded meadows with only small (1 m^2) pools of standing water. *Source* patches were considered all breeding sites that contained 1 year-old juvenile frogs or breeding sites where 1-year-old juvenile frogs were found in adjacent habitats within 300 m in any year between 1995 and 1998. I defined *sink* patches as all breeding sites without 1-year-old juvenile frogs within 300 m and all non-breeding habitats.

Local Habitat Conditions

Before considering the effects of landscape structure, I first evaluated the effect of local habitat on *R. luteiventris* abundance. I reduced the number of habitat variables using Principal Components Analysis with a Varimax rotation. Factor scores were saved and used as independent variables in multiple linear regression analysis to predict the abundance of *R. luteiventris* tadpoles and 1+year-old postmetamorphic individuals in each site. I log transformed tadpole and frog abundance to meet assumptions of normality and homoscedasticity. However, tadpole abundance was so highly skewed that I further tested the relationship between tadpole abundance and habitat factors using non-parametric Spearman's Rho rank correlation coefficients. The results were consistent with the regression analyses.

Landscape Complementation

The influence of landscape complementation on *R. luteiventris* populations was evaluated by comparing the number of frogs in breeding ponds at increasing distances from their overwintering sites in Skyhigh Basin. To test the hypothesis that breeding site populations would decrease with increasing distance from the nearest overwintering site, I used non-parametric Spearman's Rho test of the rank correlation coefficient. Non-parametric tests were used because the small sample size and skewed distribution of frog densities. Site L3 was an outlier in this analysis and influenced the result. I ran the analysis again without the outlier.

Landscape Supplementation

To examine the influence of landscape supplementation on *R. luteiventris* populations, I compared the number of frogs to the area of littoral zone or riparian habitat in all sites in Skyhigh Basin. To test whether *R. luteiventris* abundance was associated with the shoreline area of suitable habitat in Skyhigh Basin, I used simple linear regression. Frog abundance was log transformed to meet assumptions of normality.

To evaluate the effect of resource supplementation on frog size, I compared the SVL of female frogs resident to site L3 with female frogs that migrated to surrounding summer foraging areas during the summer. To test this pattern, I used a two-factor Analysis of Variance (ANOVA) with migratory behavior and year as factors and female frog SVL (July surveys only) as my dependent variable.

Because the age structure of a frog population can affect the average frog size in a population, I compared the age structure of frogs in each breeding site using skeletochronology as described by Reaser (2000). I compared the size and age of frogs in different basins using a multiple ANOVA and Tukey's tests. Finally, to assess the influence of frog density on frog size, I plotted the average frog size on frog density for each breeding population in the study area. The SVL of frogs in breeding sites of varying frog densities were compared using simple linear regression.

Neighborhood Effects

To examine the influence of a habitat neighborhood on *R. luteiventris* abundance, I tested whether surrounding fishless habitat had more of an influence on spotted frog populations than just available habitat at 250 m concentric intervals away from each site, but within the same local watershed. To evaluate the influence of surrounding habitat on each site, I first tested the relationship between the area of lentic habitat surrounding each site and the abundance of *R. luteiventris* using multiple linear regression, respectively. The influence of distance and area of surrounding habitat was evaluated by testing area of habitat in progressively larger 250 m rings around each site. To determine if fishless habitat has more of an influence on frog populations than habitat in general, I repeated the analysis using area of fishless habitat. The tests for area and for fishless area were then compared. I tested the probability of sink occupancy in relation to the distance from the nearest breeding site using logistic regression. To evaluate whether frog abundance in sinks decreased with increasing distance from the nearest breeding site, I plotted frog abundance against straight-line linear distance from the nearest breeding site. I tested the relationship with simple linear regression after log transforming both dependent (frog abundance) and independent variables (distance to nearest breeding site) to meet normality and homoscedasticity. All analyses were performed on SPSS v. 10.0 software (SPSS Inc, Chicago, IL). I considered relationships significant based on a 0.05 probability criterion.

RESULTS

Influence of Local Habitat Characteristics

Rana luteiventris adults were widespread in the study area, occurring at 79% and breeding in 48% of the 101 lentic sites. *Rana luteiventris* bred in a variety of ephemeral and permanent palustrine and lacustrine habitats, from the smallest pools (0.003 ha) to the largest lakes (35 ha; Figure 1). Measured habitat variables grouped into three factors in a principal components analysis, explaining a total of 65% of the variance (Table 3). The abundance of tadpoles and juveniles+adults increased with increasing values of factor one (Table 4). Greater numbers of frogs were found in sites with more silt substrate, less rock substrate, at least 5% of the shoreline with emergent vegetation, slightly warmer water temperatures, and at lower elevations.

Table 3. Rotated (Varimax) principal components matrix of measured habitat variables for 101 lentic sites in the study area. Factor 1 explained 27% of the variance in habitat, factor 2 explained 23% and factor 3 explained 15%. Bold loading scores indicate which habitat variables were associated with each factor (based on scores less than -0.5 or greater than 0.5), their magnitude and direction.

	Component		
Variable	**1**	**2**	**3**
Elevation	**-.593**	-.003	.294
Surface Area	-.015	**.896**	.053
Maximum Depth	-.196	**.835**	-.183
Water Temperature	**.308**	-.127	.021
% Forested Shoreline	.180	-.007	**-.851**
% Grass/Sedge Shoreline	.295	-.215	**.810**
% Rocky Substrate	**-.883**	.237	-.086
% Silt Substrate	**.863**	-.259	.117
>5% Emergent Veg.[1]	**.692**	-.000	.046
Fish Present[1]	-.273	**.761**	-.104

[1] Dichotomous Variable

Table 4. Multiple linear regression analysis of tadpole and juvenile+adult *R. luteiventris* abundance in relation to each factor score (see Table 2).

Life Stages	**Sites**	**Adj R^2**	**$F_{3,72}$**	**[1]*P***	**Variables**	**B**	**[2]*P***
Tadpole	101	0.058	3.039	0.033	Factor 1	0.286	0.011
					Factor 2	-0.170	0.126
					Factor 3	0.009	0.937
Juvenile/adult	101	0.061	3.182	0.027	Factor 1	0.215	0.003
					Factor 2	0.024	0.732
					Factor 3	0.019	0.790

[1] P = omnibus model probability F-statistic

[2] P = univariate probability t-statistic

The regression analysis between tadpole abundance and factor one violated assumptions of normality and homoscedasticity (even after log transformation), but Spearman's rho rank correlation, which does not require distributional assumptions, gave similar results (r_s=0.255, *P*=0.010, N=101).

Influence of Landscape Structure

Landscape Complementation

In Skyhigh Basin, the abundance of *R. luteiventris* in breeding ponds decreased with increasing distance to the nearest overwintering site (r_s=-0.818, *P*=0.024, N=7; Figure 2). However, this relationship was influenced by site L3. When site L3 was excluded from the analysis, the relationship was no longer significant, but still showed a negative trend (r_s=-0.754, *P*=0.084, N=6).

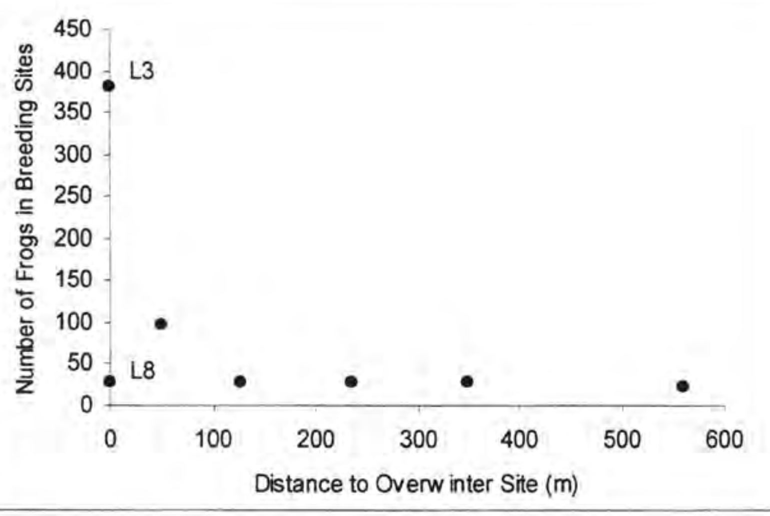


Figure 2. Relationship between *R. luteiventris* abundance in breeding sites and distance to the nearest overwintering site in Skyhigh Basin.

Landscape Supplementation

In Skyhigh Basin, the abundance of *R. luteiventris* was not associated with the area of suitable habitat (Adj. R^2=-0.032, $F_{1,25}$=0.188, P=0.668; Figure 3). One breeding site (L3) had 13.6 times the median number of frogs in other breeding sites in Skyhigh Basin (median, 28 frogs). Some of this difference may be explained by local habitat characteristics of site L3 (see Chapter I), however site L3 also had the highest rate of migration. In simple linear regression analysis, including all basins in the study area, the density of frog populations predicted dispersal rate (males, Adj. R^2=0.68, $F_{1,36}$=79.7, P<0.001; females, Adj. R^2=0.61, $F_{1,36}$=58.7, P<0.001). However, a detailed study of adult frog movements in Skyhigh Basin revealed that most adult frog movements were seasonal migrations and not one-way dispersal events. Frogs that migrated up to 1100 m from site L3 to reach summer ranges (foraging areas) returned in the fall (see Chapter I).

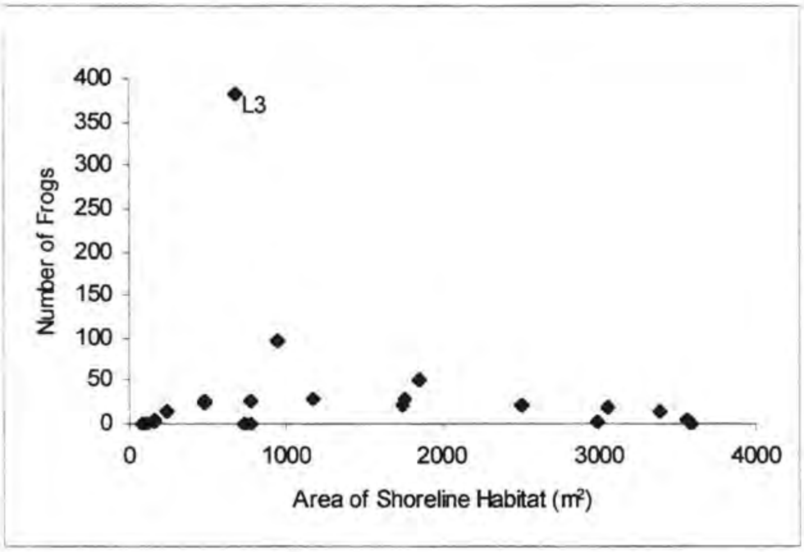


Figure 3. Relationship between *R. luteiventris* abundance and the area of suitable habitat at each site in Skyhigh Basin.

In a two factor ANOVA of migratory behavior and year on frog size, female frogs that migrated from site L3 to summer ranges (supplemental foraging) were significantly larger than year-round resident females of site L3 (Figure 4), and 1997 females were larger than 1995 and 1996, but the interaction of migratory behavior and year was not significant ($F_{5,188}$=8.297, P<0.001). Skeletochronology age estimates indicated that the age structure of L3 was not skewed toward younger individuals compared to the age structure of other breeding sites. However, across all basins, the size of female frogs decreased as the density of *R. luteiventris* increased at a site (Adj. R^2=.309, $F_{1,16}$=8.610, P=0.010; Figure 5).

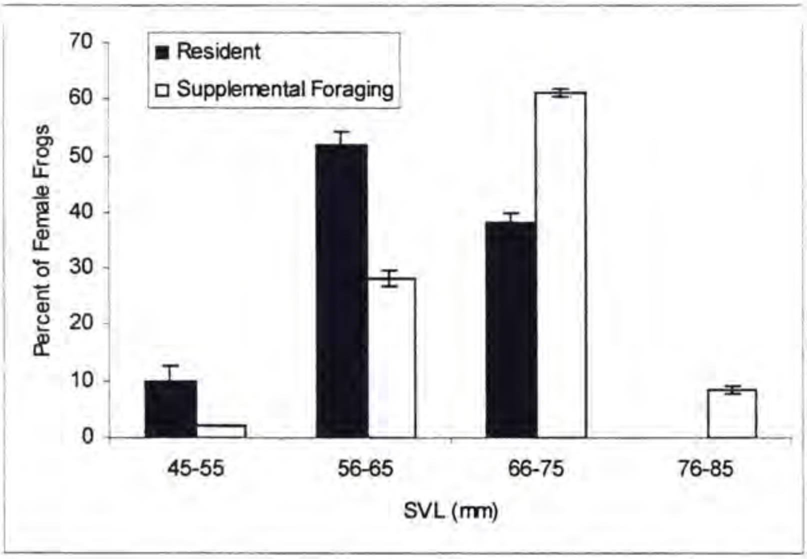


Figure 4. Comparison of the frequency of frogs in 10 mm SVL categories in relation to the migratory behavior for female *R. luteiventris* associated with site L3 in Skyhigh Basin. Yearly variance in frequency (1995-97) is shown as standard error bars.

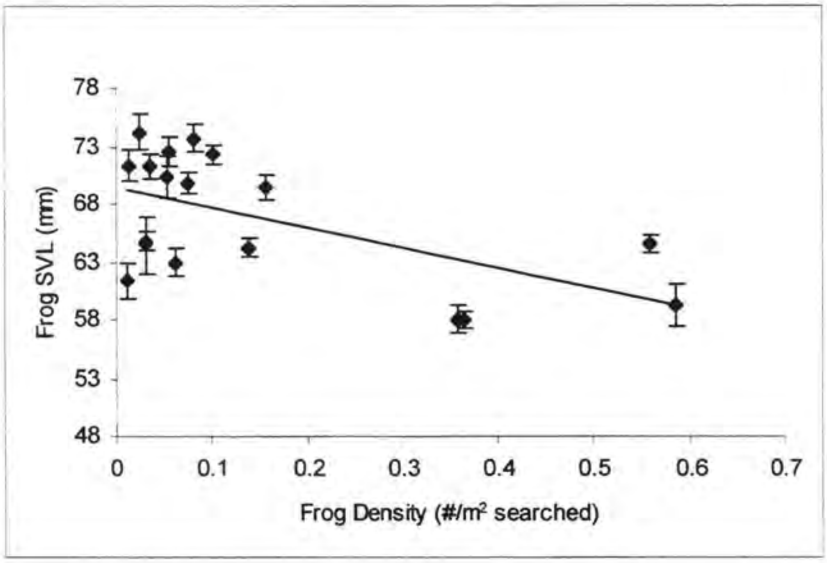


Figure 5. Size of female *R. luteiventris* in relation to the density of frogs at each breeding site in the study area. Significant regression lines are shown.

Neighborhood Effects

Spotted frog abundance in a site was positively associated to the total amount of lentic habitat in a basin (>750 m from each site; Table 5). However, frogs were more abundant in sites with greater amounts of fishless habitat within 500 m, but not greater amounts of habitat within 500 m (Table 5). Because fishless sites were more

Table 5. Statistical summary of individual regression analyses of the relationship between frog abundance and the area of habitat or area of fishless habitat in 250 m concentric rings away from each site. F and P values are for the model, after each ring was added to the analysis.

	Area All Habitat		**Area Fishless Habitat**	
Distance From Site (m)	***F***	***P***	***F***	***P***
0-250	0.77	0.382	14.83	**<0.001**
0-500	0.49	0.616	9.13	**<0.001**
0-750	0.56	0.640	7.04	**<0.001**
0-1000	4.70	**0.002**	5.37	**0.001**
0-basin	3.73	**0.004**	4.46	**0.001**

frequently source populations, I examined differences in frog abundance among sink populations (those with no juveniles within 300m) in relation to the distance from the nearest breeding site. Across all basins, the probability that *R. luteiventris* occupied sink habitats decreased significantly with increasing distance from the nearest source (logistic regression model X^2=8.101, df=1, *P*=0.004). The number of frogs ($\log_{10}$ y plus one) in sink populations decreased significantly as the linear distance from the nearest breeding site increased (Adj. R^2=0.05, $F_{1,96}$=6.641, *P*=0.011; Figure 6). However, this result should be viewed with caution as the data were highly variable even after transformations. Nonetheless, sink populations greater than 600 m from the nearest breeding site were rarely occupied (Figure 6).

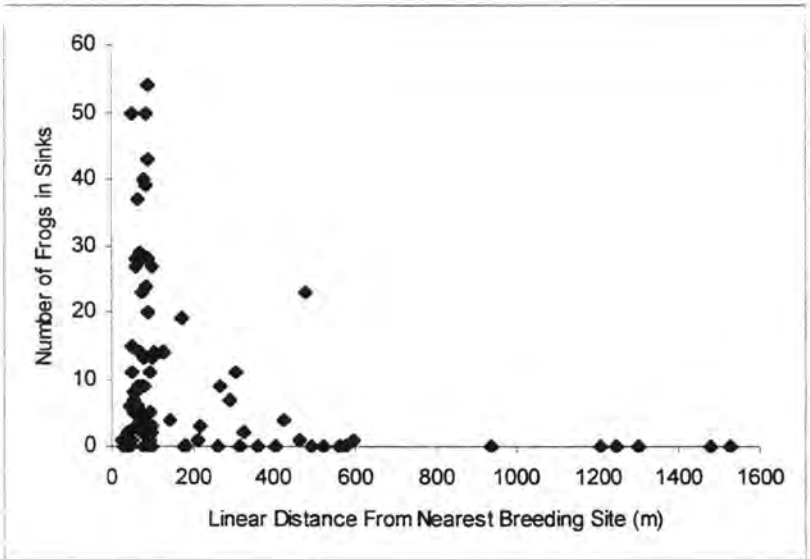


Figure 6. Relationship between *R. luteiventris* abundance in sink habitats and the distance to the nearest breeding population for all sinks in the study area.

DISCUSSION

Landscape structure can have strong influences on the age structure and dynamics of animal populations, especially for species that cannot obtain all of their required resources within breeding habitat (Pearson 1993, Solbreck 1995, Law and Dickman 1998). In particular, the effect of landscape structure depends on the dispersal behavior of the organism. Animals with low dispersal distances may be more strongly influenced by local habitat characteristics than by landscape structure (Driscoll 1997). Similarly, high dispersal distances also may decrease the effect of landscape structure on local population size, while intermediate dispersal distances and complex habitat use patterns may be most influenced by landscape structure (Fahrig and Paloheimo 1988b). Most amphibians, especially anurans (frogs and toads) are generally considered to have intermediate dispersal abilities compared to other vertebrate taxa of similar size (Sinsch 1990).

Only recently have researchers begun to examine the effects of landscape structure on the dynamics of amphibian populations and metapopulations (Sjögren 1991, Vos and Stumpel 1995, Vos and Chardon 1998, Pope et al. 2000). Understanding the influence of landscape complementation is difficult because it requires detailed information on the habitat use patterns of animals in a landscape as well as the composition and physiognomy of the habitat patches. After 3 years of intensive monitoring, including repeated mark-recapture and radiotelemetry, I was able to identify the habitat use patterns of *R. luteiventris* in a mountain basin (Chapter I). This basin provided a first test for the influence of landscape complementation on *R. luteiventris* populations. This limited data set suggests that breeding populations are smaller with increasing distance from overwintering sites. This may be related to increased mortality of juveniles and adults that have to migrate longer distances; migrating frogs are exposed to predators and may vulnerable to dehydration. Distance to suitable hibernation sites has been shown to affect reproductive success in other taxa (Solbreck 1995), but few studies have examined this spatial relationship in amphibian communities.

Variability in local patch conditions may override the effects of landscape structure on population density. For example, I suspect that site L8 in Figure 2 (the other breeding site that also was an overwintering site) may have been an outlier because it was the coldest, most isolated site in Skyhigh Basin. Across all basins, water temperature was the only habitat variable that was significantly associated with *R. luteiventris* breeding (χ^2=9.796, df=1, P=0.002). In Skyhigh Basin, tadpole density was significantly lower in colder sites (r_s=0.893, P=0.007, N=7). The low densities of frogs in site L8 were more likely a function of local conditions (cold water temperatures) than landscape physiognomy. When I exclude site L8 from Figure 2, there is an inverse negative relationship between breeding pond abundance and distance to the nearest overwintering site. Additional research, with larger sample sizes, is needed to adequately test this relationship.

Landscape complementation may play an important role in amphibian population dynamics and thus has conservation applications. For example, ignoring landscape structure may mask the effects of metapopulation structure on local population density. Pope et al. (2000) found that when summer habitat was not included in Poisson regression models predicting leopard frog (*Rana pipiens*) density, then the metapopulation structure (number of occupied ponds in the surrounding landscape) was no longer a significant predictor of frog density. They concluded that summer habitat for *R. pipiens* plays an important role in local population density and thus needs to be included in metapopulation models. Similarly, common frogs (*Rana temporaria*) in Sweden were more likely to breed in ponds that were closer to suitable summer habitats (ungrazed grassland and forests)(Loman 1988). In *Rana dalmatina* breeding sites in Denmark, researchers found nearly exponentially fewer numbers of egg-clutches with increasing distance to forest (Wederkinch 1988).

Habitat patches are generally expected to support larger populations as they increase in size (Diamond 1975, Bender et al. 1998). For this reason, I expected the largest *R. luteiventris* populations to be in the largest breeding sites. However, I did not find an association of frog abundance and breeding site size, nor have studies on other ranids (Wederkinch 1988). An alternative explanation is that the local habitat characteristics at very large breeding populations are more favorable for frog reproduction. In Skyhigh Basin, site L3 indeed has different habitat characteristics than other breeding sites (see Chapter I). For example, site L3 contained macrophytes, had an algal and silt substrate, and was fed by at least 5 springs that created an extensive perennially flooded shoreline composed of sedges, sphagnum, and algal mats. This was the only breeding pond in Skyhigh Basin that had a constant water level all year. The hydroperiod in other breeding ponds was more variable and tended to steadily decrease all summer, but filled slightly after each rain event. Some lake levels dropped over 2 m in 8 weeks.

However, local habitat characteristics do not completely explain the abundance of frogs in site L3 because this breeding site was not isolated, nor did all of the frogs remain in site L3 all year. Investigations of frog movements in this basin found that up to 25% of the frogs in site L3 migrate to flooded meadows, ponds, and lakes to forage during the summer (see Chapter I). Therefore, landscape supplementation, or the use of resources in surrounding habitats by individuals in one population, may explain why this population was so large despite the limited space available.

I predicted that if resource supplementation was occurring, then frogs that supplemented their diets in surrounding habitats would be larger. Because larger female frogs have larger clutch sizes (Joly 1991), then females that supplemented their diet could contribute more offspring to the population than resident females. Frogs that migrated from site L3 to summer habitats were significantly larger than the frogs that remained at site L3 suggesting that they may be supplementing their diet in habitats with lower frog density and thus less competition for available prey resources. There are at least two alternative explanations to this difference in size of migratory versus non-migratory females. First, female frogs that remained in L3 may have been younger than the migratory females (although age structure analysis does not support this). Second, non-migratory females may have bred that year. However, if this were the case, the weight of non-migratory females would be lower, but their size would be comparable to migratory females. I did not observe this pattern. Thirdly, those that remained behind may have been weaker or had lower hormone levels. Regardless of the reason why frogs are smaller in site L3, landscape supplementation seems to be occurring.

Landscape complementation and supplementation may be particularly applicable for animals living at the limits of their geographic range where environmental conditions challenge the physiological capabilities of most animals. For example, in the northern Rocky Mountains, relatively few amphibians live above 2000 m in elevation (Nussbaum et al. 1983, Leonard et al. 1993). Amphibians living at these elevations must endure short, dry summers with widely fluctuating daily temperatures and long, cold winters when lakes and ponds remain ice-covered for 8 to 9 months. These harsh environmental conditions result in slower amphibian growth and longer time to metamorphosis, older age at first reproduction, decreasing frequency of reproduction, and increased longevity (Anderson 1967, Licht 1975). To be successful in this inhospitable environment with such a short growing season, high elevation amphibians may have to choose specific habitats that maximize their energetic uptake, minimize their physiological stresses (e.g., dehydration, temperature regulation, respiration), and avoid predation.

Although Dunning et al. (1992) distinguished neighborhood effects as a separate landscape process, all landscape effects could be considered subcategories under neighborhood effects. Therefore, the data with which I tested this hypothesis may also have been influenced by landscape complementation and landscape supplementation. Nonetheless, frog densities were more strongly associated with the amount of nearby fishless habitat than the amount of nearby habitat in general. I suspect that this relationship was mostly the result of source-sink dynamics between fishless and fish-containing sites. Regardless of whether they fit my definition for a source, nearly all fishless sites had higher densities of frogs than fish-containing sites (see Chapter II). Because dispersal was significantly positively associated with frog density, sites with higher densities (generally fishless sites) contributed the most individuals to nearby wetlands compared to sites with lower densities (generally fish-containing). Therefore, the amount of fishless habitat in population's neighborhood had a greater affect on population density than the total amount of habitat in the neighborhood.

Based on movement patterns (Chapter I), it appears that *R. luteiventris* in this high-elevation region may live in some sort of source-sink population dynamic because the probability of sink occupancy was negatively associated with the distance to nearest source. Other amphibian studies have found that the number of individuals moving between ponds decreases rapidly with increasing distance between them (Reading et al. 1991). European studies on amphibian species indicate that occupied ponds are always <1 km from other occupied ponds, while unoccupied ponds are usually more isolated (Vos and Chardon 1998). This research indicates that *R. luteiventris* density in sink populations declines rapidly with increasing distance from the nearest breeding site and ponds >600 m from the nearest breeding site (or 1050 m from the nearest source) are unoccupied.

Although disturbance (abiotic) factors often contribute to the poor success of a population, predator-prey dynamics may also limit prey populations (Taylor 1990, Pulliam and Danielson 1991). In this study, almost all lakes with predatory fish appeared to be population sinks for *R. luteiventris* (few juveniles observed despite annual frog reproduction). Lakes with fish had few juveniles and adults relative to the number of tadpoles hatched each year and many of the adults were colonists from nearby fishless source populations (see Chapter I). Animal populations whose reproduction and immigration insufficiently balances mortality and emigration are generally considered sink populations (Pulliam 1988, Pulliam and Danielson 1991). Although sink populations can be a drain on source populations, the presence of some sink populations can actually increase the persistence of surrounding populations by providing a pool of colonists (Howe et al. 1991), an interaction particularly important for source-sink and rescue-effect metapopulations (Levins 1970, Boorman and Levitt 1973, Hanski and Gilpin 1991, Hanski and Simberloff 1997).

One of the limitations of these tests of Dunning's hypotheses is that I only considered distance as a metric of landscape physiognomy. Other measures of landscape structure are also clearly important. For example, the composition of habitat patches can have strong influences on resource use. Although I analyzed local habitat characteristics, I did not measure all important habitat characteristics such as prey composition and density, and density of all potential predators present. I also did not measure the characteristics of the matrix separating habitat patches. By spatially characterizing habitat quality (such as assigning values to different resource patches and matrix), one could examine the influence of landscape composition on populations. Several studies have found that the composition of a landscape, such as the amount of suitable terrestrial habitat (e.g., woodland, grassy meadows, moorland), can influence amphibian populations (Laan and Verboom 1990, Vos and Stumpel 1995, Vos and Chardon 1998, Pope et al. 2000).

Another measure of habitat structure that may be important to consider is the connectivity of habitat patches. For ground dwelling species, habitat patch connectivity is a combination of the distance between patches (the metric used in this paper) and the resistance of the matrix between patches (Merriam 1991, Taylor et al. 1993). The resistance of the matrix could be mapped as a gradient of movement probabilities between all resource patches based on biophysical characteristics of the land and biology and behavior of the organism (Fahrig and Paloheimo 1988b, Henein and Merriam 1990). One of the earliest telemetry studies on anurans found that common toads (*Bufo bufo*), migrating to and from their spawning site, traveled through grassland faster than through forested areas (Van Gelder et al. 1986). Future research on the influence of landscape composition and matrix resistance to amphibian movements will greatly improve understanding of the effects of landscape structure on amphibian population dynamics and persistence.

This paper demonstrated that amphibian populations are not only influenced by local habitat conditions, but also the surrounding landscape. The distance that individuals had to move between non-substitutable habitat patches (breeding and overwintering sites) appeared to have some influence on the size of the population, as did the proximity and use of foraging areas. In this study area, the local frog populations were strongly influenced by surrounding habitat conditions, namely the availability of fishless habitat. As fish predators reduce frog populations, fewer individuals are available to emigrate to surrounding populations. Water bodies more than 600 m from the nearest breeding site had a lower probability of occupancy, further supporting the importance of neighborhood interactions on amphibian population size. Given this information, conservation efforts to protect amphibian populations should consider the proximity of suitable habitats and adjacent populations that may be important for maintaining local populations or metapopulations (Marsh and Trenham 2001).

Summary and Management Recommendations

Summary

The primary goal of this study was to better understand the effects of fish stocking on high-elevation amphibian populations. Research on the distribution of introduced trout (*Oncorhynchus mykiss x O. m. aguabonita* hybrids, *Salvelinus fontinalis,* and *Salmo trutta*) and mountain yellow-legged frog (*Rana muscosa*) populations in Sequoia and Kings Canyon National Parks and John Muir Wilderness in California had provided convincing evidence that introduced trout may be contributing to the decline of montane amphibian populations (Bradford 1989, Bradford et al. 1998, Knapp and Matthews 2000). To evaluate whether fish stocking was having similar effects on other amphibian species in other geographic regions, I initiated this research with support from the Aldo Leopold Wilderness Research Institute in 1995.

The results of this study indicate a strong negative correlation between the presence of introduced trout (*Oncorhynchus clarki, O. mykiss, and O. m. aguabonita*) and the densities of all life stages of Columbia spotted frogs (*Rana luteiventris*) and larval long-toed salamanders (*Ambystoma macrodactylum*) (Chapter II). Even after controlling for habitat differences between fish-containing and fishless sites, amphibian densities were significantly lower in lakes with fish compared to similar fishless sites. These results are in agreement with the results of research from the North Cascades National Park in Washington and Bitteroot Mountains in Montana that also indicated a negative effect of introduced trout on long-toed salamanders (Tyler et al. 1998a, Funk and Dunlap 1999). This was the first study indicating that

R. luteiventris also may be negatively affected by fish, confirming suggestions to this effect by other researchers (Bull and Hayes 2000, Reaser 2000).

There are several possible mechanisms that may explain negative correlations between introduced fishes and amphibians. Diseases may be introduced with hatchery fish that can be transmitted from fish to amphibians, such as saprolegnia fungus and iridoviruses (Blaustein et al. 1994, Mao et al. 1999). Introduced fishes may compete with amphibians for limited prey resources in oligotrophic lakes (Efford and Tsumura 1973). Many introduced fishes are known predators of amphibians, including larval, juvenile, and adult life stages (Emery et al. 1972, Hayes and Jennings 1986, Semlitsch 1988, Luecke 1990, Liss et al. 1995, Braña et al. 1996, Gamradt and Kats 1996, Resetarits 1997, Simons 1998, Tyler et al. 1998b).

Although my research did not specifically address the different possible mechanisms causing the negative correlations between introduced trout and amphibians, I did make several observations that are noteworthy. Of the possible explanations, I can rule out saprolegnia fungus because amphibian egg viability, which is reduced by saprolegnia infestation (Blaustein et al. 1994), was not lower in lakes with fish compared to fishless lakes. Iridoviruses could have decreased survival of all life stages of amphibians in lakes with fish, but very few sick and dying amphibians were observed. Competition with fish for macroinvertebrates could negatively affect postmetamorphic life stages of *R. luteiventris* and competition for macroinvertebrates and zooplankton could affect larval long-toed salamanders. Trout stomach content analyses revealed that trout preyed heavily on both aquatic and terrestrial macroinvertebrates, while only a few fish were captured with zooplankton in their stomachs. Frog and salamander stomach contents were not analyzed, but known prey items of *R. luteiventris* (Turner 1959) and *A. macrodactylum* (Anderson 1968, Tyler et al. 1998a) from similar elevations overlap with those found in the stomach contents of trout in this study (Hoffman and Pilliod 1999). Therefore, some competition between amphibians and trout may be occurring. However, frogs and salamander larvae were not smaller in lakes with fish compared to similar life stages in nearby fishless water bodies suggesting that food resources are not limiting (or are at least comparable) in water bodies with fish

Based on my research, I feel that predation by trout is the mostly likely explanation for the low numbers of amphibians observed in lakes with fish. Other predators were observed in the study area, including western terrestrial garter snakes, ravens, Clark's nutcrackers, predacious aquatic insects, otters, coyotes, and foxes, but one would expect the effects of these predators to be similar in fish-containing and fishless water bodies. Trout captured in the study area ranged in size from 50-405 mm fork length and were most likely large enough to consume larval and juvenile life stages of *R. luteiventris* and *A. macrodactylum*. In northern California, a small brown trout (~200 mm fork-length) was observed consuming an adult Cascades frogs (50 mm SVL) shortly after the frog was released into a stream (Simons 1998). This suggests that even smaller adult spotted frogs may be vulnerable to trout predation. In this study, I examined the stomach contents of 490 trout removed from stocked lakes. No amphibian remains were found in these trout stomach contents, but I did find three recently metamorphosed spotted frogs in the stomach of an adult female cutthroat trout (~300 mm fork length) removed from a historically fishless lake

(Alpine Lake) that had been experimentally stocked with 22 adult trout (250-380 mm) in 1996. This indicates that trout will prey on spotted frogs in high-elevation lakes. *A. macrodactylum* larvae have been found in the stomach contents of trout in other high-elevation lake studies (Liss et al. 1995).

Although the results of my research and others indicate that introduced fish may be negatively affecting amphibian populations in montane lakes that have been stocked with fish, these results do not explain how fish stocking could lead to the extirpation of amphibians from entire watersheds where fishless habitats still exist. In an attempt to explain why mountain yellow-legged frog populations had disappeared from locations not inhabited by fish (Bradford et al. 1994), Bradford et al. (1993) hypothesized that the presence of introduced fishes in waters separating fishless sites had increased the isolation of remaining *R. muscosa* populations. Bradford based this hypothesis on extinction theory that small, isolated populations have higher risk of extinction and decreased chance of recolonization than larger populations in closer proximity to other populations (Simberloff 1994). The assumption that extinction and recolonization is associated with isolation gradients of frog populations has been supported by several broad scale studies. For example, Sjögren (1991) demonstrated that pool frog (*Rana lessonae*) populations that were isolated by more than 1 km went extinct, while less isolated populations tended to persist. Populations that are not isolated may still go extinct, but are often frequently recolonized (Carlson and Edenhamn 2000), or continue to persist due to immigration and the rescue effect (Brown and Kodric-Brown 1977, Gill 1978, Sinsch 1992, Sjögren-Gulve 1994).

Although Bradford et al. (1993) estimated that fishless lakes in Sequoia and Kings Canyon National Parks were 10 times more isolated by fish now than historically, he did not have evidence that fish actually presented a barrier to dispersal. By examining the movement patterns of *R. luteiventris*, I found that adults successfully traveled between fishless sites along streams occupied by trout. Furthermore, *R. luteiventris* used some terrestrial migratory routes and thus did not require streams for travel. These results suggest that introduced trout did not present a barrier for the movement of adult *R. luteiventris*. Trout may have preyed upon dispersing juvenile frogs, and thus created a migratory barrier for this life stage, but my capture records of juveniles were too low to fully address this hypothesis adequately.

Even though trout did not appear to isolate *R. luteiventris* populations in fishless sites, I noticed that frog populations in fishless sites in heavily stocked basins were unusually small compared to basins with more fishless habitat. To study this pattern, I compared the average density of amphibian populations in fishless habitats in basins with varying levels of trout occupancy. I hypothesized that if fishless water bodies were uninfluenced by surrounding fish-containing lakes, given that their habitat characteristics were similar, a fishless water body in a basin with few lakes occupied by trout should support similar densities of amphibians as a fishless water body in a different basin with many lakes occupied by trout. My results indicate a strong negative correlation between the percent surface area of water bodies containing trout in a basin and the average density of both postmetamorphic *R. luteiventris* and second and third-year *A. macrodactylum* larvae in fishless water bodies in a basin. As the percent surface area of water bodies occupied by trout increased in a basin, the average density of older life stages of amphibians in fishless sites in that basin decreased. This result suggests that negative effects of introduced trout somehow also negatively affect amphibian populations in fishless water bodies in a basin.

There are several possible explanations for this relationship. Despite a common misconception that amphibians hatch, live, and die in the same body of water, I demonstrated that *R. luteiventris* move among different habitats over the course of a year, with some females traveling over 1000 m to reach summer habitats (Chapter I). One of the most important findings of my movement study was that *R. luteiventris* often overwintered in habitats occupied by trout. Winter predation on amphibians is known to occur even under ice (Emery and others 1972, J. Griffith, personal communication). Predation on postmetamorphic *R. luteiventris* by trout during winter may explain why lakes with fish had lower recruitment and fewer adults than fishless lakes.

Trout predation during winter also could explain why basin fish stocking appeared to negatively affect frog populations in fishless water bodies. Frogs that bred in shallow, fishless wetlands often migrated to deep, fish-containing lakes to overwinter, and thus were exposed to predation by trout during winter. Therefore, winter trout predation on frogs that came from surrounding fishless wetlands could reduce frog recruitment in fishless sites as well and explain why fishless water bodies had lower densities of overwintering life stages of amphibians in heavily stocked basins compared to basins with fewer stocked lakes. Keep in mind that heavily stocked basins had fewer deep, fishless water bodies than basins with fewer stocked lakes. This was demonstrated in Chapter II. In two heavily stocked basins (>96% surface area of water bodies occupied by trout; Glacier and Sheepeater) with only shallow (<2 m) fishless habitats remaining, I did not observe any juvenile frogs in 4 years of surveys, despite yearly spotted frog reproduction in fishless habitats in these basins. I suspect that the adults, juveniles, and recently transformed frogs in these basins migrated to adjacent deeper lakes to overwinter. In these basins, all of the deeper lakes contained fish. Based on the age structure of spotted frogs in these basin populations (as determined using skeletochronology of captured animals), these heavily stocked basins have not had a successful reproductive year for spotted frogs since ~1991. Given the longevity of the frogs (12-14 years) and the fact that no marked individuals moved between basins, *R. luteiventris* could disappear from these basins within the next 5-10 years.

The effect of landscape physiognomy (as measured by straight-line distance) on amphibian use of complementary (non-substitutable) resources also appeared to influence amphibian populations (Chapter III). The further frogs had to travel between breeding sites and overwintering sites, the lower the density of frogs in breeding sites. In Skyhigh Basin, frogs migrated considerable distances to reach fishless overwintering sites, possibly resulting in decreased recruitment of juveniles in distant populations due to the higher risk of mortality associated with travel from breeding sites to overwintering sites immediately after transforming from tadpoles into juvenile frogs (Chapter I). The spatial arrangement of fishless overwintering habitat and differences in survival of individuals in fishless versus fish-containing overwintering sites needs to be addressed in future studies.

Another possible explanation for the negative basin-level effects of fish stocking is that source populations of amphibians in heavily stocked basins may have already been extirpated. In Chapter III, I showed how the probability of occurrence and abundance of spotted frogs decreased with increasing distance from the nearest source population (and breeding site). If source populations have been eliminated from lakes now occupied by fish, then the remaining amphibian populations in surrounding water bodies are now further from the nearest source. Therefore, basins with more lakes stocked with fish would be more likely to have increasing distances between remaining fishless habitats, as well as increasing distances to the nearest source population.

Limits of Inference

Inferring the generality of results requires some knowledge of the spatiotemporal grain and extent of a study, which are defined by the resolution and scope of the data, respectively (Allen and Hoekstra 1992). The grain or lower limit of inference in this study is the individual animal located to the minute. The extent or upper limit of inference of this study is the 11 basins in the Bighorn Crags studied for 4 years from 1995-98.

This study was not designed to generalize the results outside of the study area because neither the study area, basins, nor individual water bodies were randomly selected. The study area is located in one of the highest mountain ranges in the Frank

Church-River of No Return Wilderness (FC-RNRW) and has a different climate and annual weather patterns than other regions of the FC-RNRW and state (Finklin 1988). These climatic differences may cause amphibians in the study area to use different habitats for breeding, foraging, and overwintering than conspecifics at lower elevations or regions with higher precipitation. As a result, *R. luteiventris* and *A. macrodactylum* in the study may have different habitat requirements and thus respond differently to fish stocking than conspecifics elsewhere in their range.

In addition to the spatial limitations of this study, the relatively short duration (4 years) restricts the conclusions temporally. For example, I did not observe a successful recruitment event in two basins (Glacier and Sheepeater) during this study, but it is possible that I did not study the system long enough. Anurans have considerable reproductive potential, when a few individuals can produce hundreds and even thousands of juveniles in a good year. Because amphibian population fluctuations are often closely tied to weather, particularly drought (Pechmann et al. 1991), I compared the precipitation and temperature records from 1995-98 with the preceding 20 years using weather station data collected at a similar elevation 20 km to the southwest. The 4 years of this study were similar to the previous 20 years and 1991 (apparently the last recruitment year in some basins) was not an unusually dry or wet year. This suggests that my study was completed during "typical" weather years and thus the patterns of amphibian distribution and abundance were less likely attributed to unusual abiotic conditions than other factors, such as trout presence.

Management Recommendations

Like many ecological problems, the anthropogenic effects of trout stocking on amphibians can vary for different species and even different populations of the same species under a variety of conditions. This variability makes it difficult to make general management recommendations that will adequately protect all species and their habitats. However, research can greatly improve the evaluation and implementation of effective management actions that may balance the conservation of native species with the needs of recreational anglers. If the goal of a management action is to find this balance, then any alterations in stocking practices should strive for the lowest cost-benefit ratio in terms of decreasing threats to amphibian persistence with the fewest changes to current recreational fishing opportunities.

Possible management actions include: (1) making no changes in stocking practices, (2) ceasing stocking and possibly removing fish from some lakes, (3) reducing stocking frequency and density, (4) reducing naturally reproducing populations of fish by restricting access to spawning areas and/or gill netting, (5) changing species stocked, and (6) stocking sterile fish.

Cessation of stocking in order to restore some wilderness lakes should benefit amphibians and reduce threats to persistence as long as amphibians are able to colonize the lakes after restoration. In the Bitterroot Mountains of Montana, six of 18 stocked lakes (33%) no longer supported trout populations in 1996, following cessation of stocking in 1984 (Funk and Dunlap, 1999). Funk and Dunlap (1999) found that long-toed salamanders recolonized five of these lakes that returned to a fishless condition within two decades, even in lakes over 5 km from the nearest salamander populations. This study indicates the potential response of amphibians after fish disappear. Similar restoration efforts in California found that mountain yellow-legged frog populations went from 20 adults and 20 tadpoles to 120 adults and 1,400 tadpoles within three years of fish removal (R. Knapp, Unpublished Data).

The management question is not whether amphibian populations will respond to fish removal, but whether such drastic measures are needed. Undoubtedly, management actions involving fish removal will be unpopular for many anglers and could result in economic impacts on outfitters and guides. Fish removal could also result in less support for wilderness. Therefore, information on which amphibian populations are at risk and what are the minimum management actions needed to help reverse these threats is of utmost importance. With 4 years of data on amphibian and fish populations in the Bighorn Crags, I am in a unique position to be able to make specific management recommendations for my study area. I present these recommendations in Table 1.

My management recommendations are based on the results of this study and personal knowledge about the study area. In this study, over 40% of the stocked lakes had at least some frog reproduction, yet few of these lakes had any frog recruitment. Given a chance (i.e., reducing predation on tadpoles and juveniles), I think that amphibian populations would respond if fish were eliminated from a lake that has some amphibian reproduction. Furthermore, restoring lakes that provide overwintering habitat for amphibians can benefit amphibians both locally and potentially across a watershed. When selecting lakes to be restored, the amount of effort required should be considered. Nonreproducing fish can be eliminated from a

Table 1. Amphibian status and management recommendations for 11 basins in the Bighorn Crags, Lemhi County, Idaho. Also shown are: the number of amphibian breeding sites, the maximum number of postmetamorphic Columbia spotted frogs (CSF) and the maximum number of long-toed salamanders (LTS) observed between 1995-98, the number of fish-containing sites relative to the total number of sites, and the number of deep (>2 m) fishless sites relative to the total number of deep (>2 m) sites in each basin.

Basin	# CSF Breeding Sites	# CSF Adults & Juv.	# LTS Breeding Sites	# LTS Larvae	# Sites with Fish / Total # Sites	# Deep Fishless Sites / Total # Deep Sites	Status and Management Recommendation
Birdbill	6	84	4	98	5 / 9	0 / 5	Moderate risk of CSF and LTS extinction. Excellent fishless breeding habitat east of Gentian Lake and below Mirror Lake, but no winter habitat. Difficult to manage because of fish movement in streams. Small lake below Gentian may be able to provide winter habitat for frogs if fish removed. Poor fish condition in all lakes, but popular camping area.
Cathedral	0	13	0	0	1 / 2	0 / 1	High risk of CSF extinction. LTS may be extinct No breeding observed. Poor fishless habitat. Few management options because of size of lakes.
Glacier	2	26	1	1	7 / 7	0 / 6	High risk of CSF extinction. LTS may be extinct. No fishless habitat available. Recommend removing fish from Pothole Lake. This lake has good amphibian habitat.
Golden Trout	2	32	1	1	3 / 3	0 / 2	High risk of CSF and LTS extinction. No fishless habitat available. Difficult to manage because of movement of fish in streams. Recommend removal of fish from lower Golden Trout Lake. This lake has few angler days and is excellent amphibian habitat.
Harbor	6	245	2	512	4 / 12	0 / 3	Low to moderate risk of CSF and LTS extinction. Most of the amphibians in this basin are found in one fishless lake. Bost species should persist without intervention.
Lost	3	49	2	23	4 / 6	0 / 4	Moderate risk of CSF and LTS extinction. One good fishless breeding site. Management is difficult because of fish movement in streams. This basin has very few angler days and should be taken off the stocking schedule.

Basin	# CSF Breeding Sites	# CSF Adults & Juv.	# LTS Breeding Sites	# LTS Larvae	# Sites with Fish / Total # Sites	# Deep Fishless Sites / Total # Deep Sites	Status and Management Recommendation
Sheepeater	3	16	0	0	3 / 5	0 / 3	High risk of CSF extinction. LTS may be extinct. One good fishless breeding site (above Shoban), but no fishless winter habitat. Few management options because of size of lakes and fish movement in streams. Recommend taking basin off stocking schedule because of poor fish condition and min. angler days.
Ship Island	3	69	0	0	2 / 5	1 / 3	Low risk of CSF. LTS may be extinct. One good fishless breeding site. Ship Island Lake has refugia for frogs. No salamanders observed. Few management options because of lake size.
Skyhigh	10	833	14	415	7 / 29	4 / 11	Low risk of CSF and LTS extinction. Recommend monitoring two main source populations (site L3 and Fawn Lake).
Terrace	4	27	3	347	5 / 7	0 / 5	High risk of CSF and moderate risk of LTS extinction. One fishless LTS breeding site looks good (below Barking Fox). Difficult to manage Terrace lakes because of fish movement in streams. Recommend cessation of stocking in Barking Fox Lake.
Tip Top	13	2629	11	954	2 / 16	7 / 9	Low risk of CSF and LTS extinction. Very large populations of both species. No management changes required.

lake by simply removing that lake from the stocking schedule, while reproducing fish populations may require gill netting (Knapp and Matthews 1998), spawning habitat barriers, or even piscicides.

Other management strategies include reducing the frequency, density, species, and/or fertility of fish stocked. These actions have the potential to benefit both anglers and amphibians. In the best circumstance, densities of trout could be reduced, even to the point of providing fishless or near fishless habitats for short intervals of time (several years). This strategy may be attractive to the angling public, if larger trout are caught during periods of low fish density (when lakes are designated as "trophy waters"). If amphibians could produce a successful cohort during these intervals, this action could help sustain populations of those amphibians that are long-lived. However, this strategy does not take into consideration the stochastic variables that can greatly influence amphibian recruitment, namely weather. In addition, larger fish have a greater gape and may prey on adult amphibians that were invulnerable to smaller fish (Zaret 1980, Semlitsch and Gibbons 1988). In amphibian populations, threats to older, reproductively mature individuals may be the most damaging to a population's persistence (Green 1997). In yet other circumstances, natural fish reproduction may reduce the effectiveness of this strategy by changing the density or size structure of fish populations. Clearly, further investigation of these strategies is warranted.

Given sufficient information, I recommend approaching management actions on a basin-by-basin and lake-by-lake basis. In areas where sufficient or appropriate habitat is available, no changes in stocking programs are needed. For example, I believe the presence of fish in Tip Top Basin is having a minimal affect on amphibian populations. In some lakes, shoreline emergent vegetation may provide refugia for amphibians from fish predators, such that amphibian populations may be able to coexist with trout (Hecnar and M'Closkey 1997). I did not observe this pattern in the Bighorn Crags, but I have heard reports of this occurring in other lakes in the northern Rocky Mountains (S. Rumsey, Montana Fish Wildlife and Parks, personal communication). In watersheds where amphibian populations are at risk, restoring a few deep, fishless lakes to provide the necessary habitat requirements for amphibians may disproportionately reduce the threats of fish stocking on amphibian persistence at the basin level. I believe management actions should be taken in basins where amphibians are at risk of extinction. However, I also believe that amphibian conservation can be accomplished while maintaining recreational fishing opportunities in many wilderness lakes.

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